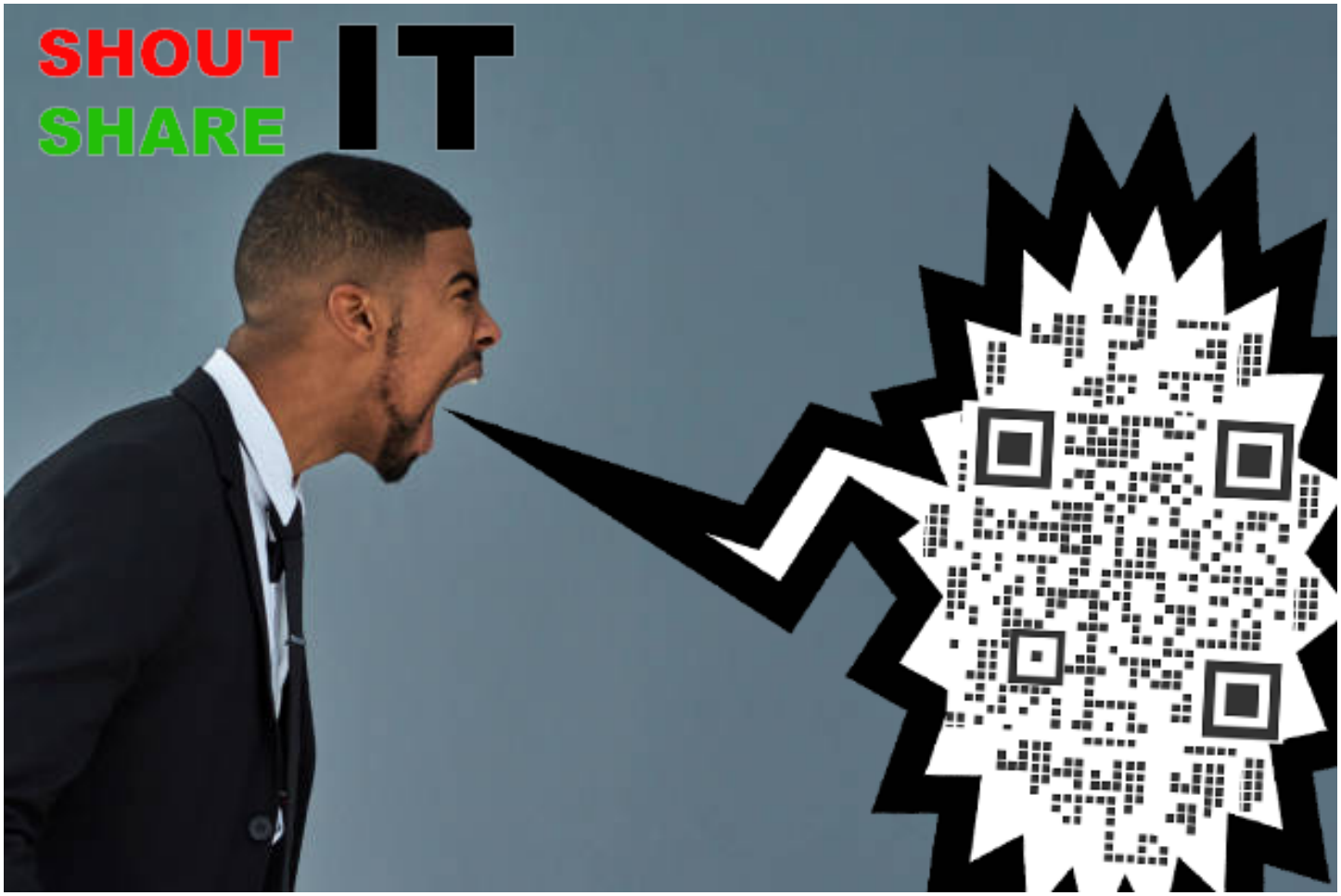
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ON THE CLARIFICATION OF LARVAL TUNA IDENTIFICATION PARTICULARLY IN THE GENUS *Thunnus*

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WALTER M. MATSUMOTO,[1] ELBERT H. AHLSTROM,[2] S. JONES,[3]
WITOLD L. KLAWE,[4] WILLIAM J. RICHARDS,[5] AND SHOJI UEYANAGI[6]

ABSTRACT

A Larval Tuna Identification Workshop was held at the Bureau of Commercial Fisheries Biological Laboratory (now the National Marine Fisheries Service, Southwest Fisheries Center), Honolulu, Hawaii, on March 2-6, 1970, to resolve conflicting views on the identification of larvae of *Thunnus alalunga* and *T. albacares* and to clarify the status of larval identification of other *Thunnus* species.

The identification of *T. alalunga* (Yabe and Ueyanagi, 1962), *T. albacares* (Matsumoto, 1958), *T. obesus* (Matsumoto, 1962), and *T. thynnus* (Yabe, Ueyanagi, and Watanabe, 1966) was agreed upon as correct, except that the description of *T. albacares* should include the appearance of black pigmentation at the tip of the lower jaw when the larva attains a length of about 4.5 mm SL and that the lower size limit of reliable identification of *T. alalunga* be set at about 4.5 mm SL until further studies indicate more precisely whether the black pigmentation at the tip of the lower jaw in *T. albacares* appears earlier. There was no difference in appearance of *T. thynnus* larvae from the Atlantic and Indo-Pacific Oceans. The identification of *T. tonggol* and *T. maccoyii* larvae was not conclusive. The larvae of *T. atlanticus* required further study.

The workshop further concurred that juveniles (13-200 mm SL) of several species of *Thunnus* may be separated by internal and external characters: *T. atlanticus* by vertebral count, *T. alalunga* by shape of first elongate haemal spine and arrangement of pterygiophores of the second dorsal fin relative to two adjacent neural spines, and *T. thynnus* by configuration of lateral line and arrangement of pterygiophores of the second dorsal fin; and that juveniles of *T. obesus* and *T. albacares* may be separated from the previous three species by arrangement of pterygiophores of the second dorsal fin, but not from each other.

The proper identification of larval tunas has been a perplexing and difficult problem for many years. Although progress in the past two decades has resulted in agreement on the identification of larvae of a number of species (*Katsuwonus pelamis, Euthynnus alletteratus, E. affinis, E. lineatus, Thunnus thynnus, T. obesus,* and *Auxis* spp.), there is still some disagreement and confusion on the identity and description of *T. alalunga* and *T. albacares.* At the present time there are two different descriptions given for *T. alalunga* (Matsumoto, 1962; Yabe and Ueyanagi, 1962). The identity of other tunas, such as *T. tonggol, T. maccoyii,* and *T. atlanticus,* has yet to be confirmed or resolved.

One of the chief problems in larval tuna identification is the difficulty in obtaining good series of larvae for study. Tuna larvae are seldom taken in sufficient numbers by the usual collecting methods, and individuals over 10 mm standard length (SL) are taken rather infrequently. Additionally, although the young of a number of tuna species are found together in many parts of the ocean, some species are localized in certain areas. Consequently, it is extremely difficult for workers in different parts of the world to have

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at hand a complete series of larvae of more than two to four species.

In an attempt to resolve the conflicting views on *T. alalunga* and to review the identification of larvae of other species of tunas, a Larval Tuna Identification Workshop was held at the Bureau of Commercial Fisheries (BCF) Biological Laboratory (now the National Marine Fisheries Service, Southwest Fisheries Center), Honolulu, Hawaii, on March 2-6, 1970. The workshop also afforded an opportunity to workers specializing on larval tuna identification to assemble specimens of the various species of tunas and to examine these together. The procedure followed at the workshop was (1) to summarize the status of larval tuna identification to date by species and (2) to evaluate the identifying characters by examining larval specimens. As time permitted, the status of juvenile tuna identification was also examined.

The participants included:

Mr. Walter M. Matsumoto, Convenor
Dr. Elbert H. Ahlstrom, Advisor
Dr. Santhappan Jones
Mr. Witold L. Klawe
Dr. William J. Richards
Dr. Shoji Ueyanagi

Dr. Jean-Yves Le Gall of the Centre Océanologique de Bretagne, Brest, France, attended the workshop as an observer.

The sessions were conducted informally with a summary of the present status of larval tuna identification, including recent developments, followed by evaluation of the various characters that could be relied upon for positive identification. Most of the sessions were devoted to direct examination of larval specimens of the various species and discussions of unpublished data offered by participants.

This report summarizes the proceedings and results of the workshop.

RECENT DEVELOPMENTS IN THE IDENTITY OF *Thunnus alalunga*

Two differing versions of the identity and description of *T. alalunga* had arisen from reliance on black pigmentation in different parts of the body. Matsumoto (1962) relied upon black pigmentation on the dorsal and ventral edges of the trunk forward of the caudal fin base, whereas Yabe and Ueyanagi (1962) relied upon black pigmentation on the tips of the upper and lower jaws and the absence of pigmentation on the trunk.

The lack of sufficient larvae fitting Matsumoto's description from areas presumed to be spawning grounds on the basis of gonad studies casts some doubt on his identification. On the other hand, good correspondence in the occurrence of larvae fitting Yabe and Ueyanagi's description with catches of adult *T. alalunga* in various areas in the Pacific seemed to support the latter identification. A study of red pigment patterns in larvae prior to preservation (Ueyanagi, 1966) reinforced Yabe and Ueyanagi's identification and description. Additional observations on red pigmentation by Matsumoto (see later discussion) confirmed Ueyanagi's results and also provided more data to enhance the reliability of red pigmentation as a supplementary character for identifying *T. alalunga*.

IDENTIFICATION OF TUNA LARVAE

With the problem of differences in the identity and description of *T. alalunga* larvae fairly well settled at the outset, there remained the tasks of evaluating the various identifying characters, not only for this species but for other tunas as well, and of describing the species at various size categories.

DEFINITION OF LARVA

In tunas, as in many other fish, it is difficult to clearly separate the larval from the juvenile stages because there is no marked metamorphosis and the usual adult characters used for species identification develop gradually and separately. It is generally accepted among workers in larval tunas that the larval stage ends when the larva has developed the full complement of spines and rays in all the fins, all the vertebrae have ossified, and the anal opening has moved back near the origin of the anal fin. For nearly all tuna species, these developments occur when the larva has attained 10 to 13 mm SL. We use this as our definition, also.

EVALUATION OF CHARACTERS

In identifying fish larvae collected in plankton nets, the easiest and perhaps the only recourse is to identify the largest stage and work down to the smallest. Unfortunately, very few tuna larvae above 9 mm SL are taken in plankton net tows so that this process cannot be followed at all times and identification, therefore, must depend upon those nonadult characters that are the most distinctive and consistent throughout the size range.

Characters that have been used in the past were reviewed and evaluated. A résumé of the usefulness of the various characters follows.

Meristic

The number of myomeres is useful in separating *Katsuwonus pelamis* (42-43) and *Euthynnus lineatus* (38-39) from other tunas, including other species of *Euthynnus*, all of which have similar numbers of myomeres (40-41). The number of fin rays and spines are not useful for separation of *Thunnus* because all species are similar in this respect.

Morphological

Shape of first dorsal fin, when completely formed, is useful to distinguish late larval stages of *K. pelamis*, *Euthynnus*, and *Auxis* from those of *Thunnus*. Preopercular spines are unreliable because they undergo rapid growth changes and position of eye relative to longitudinal axis of body needs to be determined more accurately. Distribution (number and position) of pterygiophores in the second dorsal fin in relation to neural spines is useful in separating several *Thunnus* species, but only after these bones have ossified in larvae longer than 10 mm SL. Other characters of the axial skeleton useful in identification, such as the position of the first haemal arch and the position of the zygapophyses on the vertebrae, also form late.

Measurements

Morphometrics have not been used extensively to date, although there may be some with good possibilities, such as the relations of body depth to standard length, snout length to head length, and snout length to orbit diameter. Some of the reasons for not using measurement data are that the larvae not only shrink in preservatives, but the degree of shrinkage varies in different preservatives and with duration of preservation; the distortion of the body at the time of fixing cannot be controlled; and, more important, there are too few larvae in undistorted condition for reliable measurements. Added to these are other sources of variability such as rapid changes in body parts due to growth, changes which often occur in spurts, and distension of the abdomen, as well as stretching of the body at each feeding.

Pigmentation

For the most part black pigment patterns have been the most widely used and accepted character in identifying tuna larvae. There are variations and changes in black pigment patterns on tuna larvae due to growth, but in certain areas of the body these patterns have been found to be consistent enough for identification purposes. This is particularly true of pigment patterns on the first dorsal fin, posterior half of the trunk, forebrain, and tips of both jaws. The larval size at which black pigment cells appear in certain areas of the body, especially at the upper and lower jaw tips, may be useful in separating *T. albacares* from *T. alalunga*. Red pigment patterns, although not species specific, have been useful in confirming the identification of *T. alalunga* when used in conjunction with black pigment patterns.

Of all the characters reviewed and examined, pigment patterns, both black and red, were considered to be the most reliable for identification of the larval stages, despite their known variability, when supplemented by the use of certain morphological characters such as the distribution of pterygiophores in the second dorsal fin and characteristics of the vertebral column, whenever these are developed.

VERIFICATION OF RED PIGMENTATION

Ueyanagi (1966) reported on the usefulness of red pigmentation in identifying tuna larvae. Up to then identification of tuna larvae by pigmentation had been based on black pigment only.

Ueyanagi examined 350 larvae and concluded that *T. albacares* and *T. alalunga*, which are difficult to identify by the usual diagnostic characters, could be distinguished by differences in red pigment patterns: larvae of *T. alalunga* consistently had more red pigment spots on the dorsal and ventral edges of the body and along the mid-lateral line forward of the caudal peduncle than larvae of *T. albacares;* red pigment patterns in larvae of *T. thynnus* and *T. obesus* were intermediate between those of *T. alalunga* and *T. albacares;* the red pigment pattern in *Allothunnus fallai* was similar to that in *Thunnus;* and the pattern in *K. pelamis* resembled that in *Auxis* spp. and *E. affinis* but differed from that in *Thunnus.*

To confirm these results and to provide additional information on red pigmentation in tuna larvae, the results of observations made on 432 larvae taken in Hawaiian waters during August and September 1967 were presented. Tables 1 and 2 give the number of red pigment cells along the dorsal, ventral, and lateral lines on the posterior half of the trunk and a summary of the number of larvae examined, the number of larvae observed with red pigmentation, and the mean numbers of red pigment cells at the three sites. In Table 2, the number of red pigment cells observed most frequently are given in bold face type and those observed occasionally or seldom are enclosed in parentheses.

The pigment patterns agreed generally with those reported by Ueyanagi for the species listed in the tables. Differences in the patterns were noticeable mainly in the dorsal edge of the trunk and, to a lesser extent, in the mid-lateral line. There was no significant difference in the number of pigment cells between the left and right sides of the body.

The appearance and extent of red pigment cells varied in larvae taken in night and day tows. In larvae taken at night the pigment cells were numerous, distinct, and brightly colored, whereas in larvae taken during the day the pigment cells were faintly colored, often not visible, and in many instances the pigment spots were united, forming single continuous lines. Of the species taken in both day and night tows (*T. albacares, T. obesus,* and *K. pelamis*), red pigmentation was not visible in 41.5% of the larvae taken during the day, compared with only 3.6% of the larvae taken at night. Thus, observations of red pigment cells must be made largely on larvae taken at night to reduce the effects of diel variations.

Despite the variations, red pigmentation is a useful supplementary character to either separate certain species or verify the identification made on the basis of other characters. That the red pigment pattern is not species specific is clearly seen in the similarity among *K. pelamis, Auxis* spp., and *E. affinis* and between *T. obesus* and *T. albacares*; however, it is useful in separating *T. alalunga* from the other kinds of *Thunnus.*

EXAMINATION AND DISCUSSION OF SPECIES

Thunnus alalunga and *T. albacares*

Larvae of these two species were examined together because they are the only species lacking black pigment cells on the trunk, exclusive of the caudal fin and abdomen (Yabe and Ueyanagi, 1962). Characters, including some that have not been used in the past, for separating the two species are summarized in Table 3. The larval stage was divided into two size categories, small larvae less than 10 mm SL and larger larvae 10 to 13 mm SL, because the characters used in differentiating small larvae became ineffective or obscured with growth. As mentioned earlier, pigmentation, particularly the presence of black pigment cells at the tips of the upper and lower jaws and the amount of red pigment cells on the trunk, was the most reliable character in separating larvae of the two species.

In small larvae, black pigment cells on the lower jaw tip were first observed in larvae of *T. albacares* about 4.5 to 6.0 mm SL, and often as small as 3.8 mm SL; those on the upper jaw tip were first observed in larvae about 7.0 mm SL (Figures 1 and 2, reproduced from Matsumoto, 1958[7]). In *T. alalunga* these pigment cells were

[7] The difference in developmental stages per given size in the figures by Matsumoto (1958) and Ueyanagi (1969) is due to method of preservation: Matsumoto's figures are of larvae preserved in 10% Formalin; Ueyanagi's figures are of larvae preserved in 70% alcohol.

TABLE 1.—Frequency of red pigment cells in larval tunas from Hawaiian waters, August-September 1967.

Part of body	No. of pigment cells	*Thunnus albacares*			*Thunnus obesus*			*Thunnus alalunga*			*Katsuwonus pelamis*			*Auxis* spp.			*Euthynnus affinis*		
		Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]	Left side	Right side	Percent occurrence[1]
Dorsal edge trunk	0	56	52	51.9	26	26	57.7	--	--	--	86	87	99.4	49	20	94.5	8	7	100.0
	1	42	32	35.6	16	18	37.7	--	--	--	--	--	--	2	2	5.5	--	--	--
	2	10	9	9.1	4	--	4.4	3	3	46.1	1	1	0.6	--	--	--	--	--	--
	3	4	2	2.9	--	--	--	3	3	46.1	--	--	--	--	--	--	--	--	--
	4	--	1	0.5	--	--	--	1	--	7.7	--	--	--	--	--	--	--	--	--
Total		112	96	--	46	44	--	7	6	--	87	88	--	51	22	--	8	7	--
Mid-lateral line trunk	0	4	9	6.3	11	8	21.6	--	--	--	85	86	97.7	35	16	70.0	6	7	86.7
	1	12	11	11.2	6	8	15.9	--	--	--	1	--	0.6	13	5	24.6	--	--	--
	2	45	34	38.3	11	13	27.3	--	1	7.7	1	1	1.1	2	1	4.1	1	--	6.7
	3	31	24	26.7	10	8	20.4	3	2	38.4	--	1	0.6	1	--	1.4	1	--	6.7
	4	14	14	13.6	7	5	13.6	3	3	46.1	--	--	--	--	--	--	--	--	--
	5	4	3	3.4	--	1	1.1	1	--	7.7	--	--	--	--	--	--	--	--	--
	6	1	--	0.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Total		111	95	--	45	43	--	7	6	--	87	88	--	51	22	--	8	7	--
Ventral edge trunk	0	1	--	0.5	--	1	1.2	--	--	--	1	--	0.6	--	--	--	--	--	--
	1	--	--	--	2	--	2.4	--	--	--	2	2	2.3	--	--	--	--	--	--
	2	1	--	0.5	1	--	1.2	--	--	--	3	5	4.6	4	2	8.2	--	--	--
	3	2	7	4.6	3	4	8.6	--	--	--	5	5	5.7	4	--	5.5	--	--	--
	4	6	9	7.7	7	5	14.8	--	--	--	6	4	5.7	3	1	5.5	--	1	6.7
	5	13	16	14.9	12	10	27.1	1	--	7.7	9	12	12.0	2	5	9.6	1	3	26.7
	6	19	14	17.0	8	10	22.1	2	--	15.4	8	8	9.0	3	1	5.5	3	--	20.0
	7	22	14	18.5	5	4	11.1	1	3	30.8	17	8	14.3	5	2	9.6	--	1	6.7
	8	14	12	13.4	4	3	8.6	2	--	15.4	7	12	10.8	10	3	17.8	1	2	20.0
	9	6	7	6.7	--	1	1.2	--	1	7.7	12	10	12.6	3	1	5.5	2	--	13.3
	10	7	5	6.2	--	--	--	--	1	7.7	6	10	9.1	8	4	16.4	1	--	6.7
	11	3	2	2.6	--	--	--	--	--	--	6	5	6.3	1	1	2.7	--	--	--
	12	3	1	2.1	--	1	1.2	1	1	15.4	1	4	3.9	6	1	9.6	--	--	--
	13	1	--	0.5	--	--	--	--	--	--	--	1	0.6	--	1	1.4	--	--	--
	14	2	1	1.5	--	--	--	--	--	--	2	1	1.7	2	--	2.7	--	--	--
	15	--	2	1.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	16	1	--	0.5	--	--	--	--	--	--	1	1	1.1	--	--	--	--	--	--
	17	--	--	--	--	--	--	--	--	--	1	--	0.6	--	--	--	--	--	--
	18	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	19	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
	20	1	1	1.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Total		103	91	--	42	39	--	7	6	--	87	88	--	51	22	--	8	7	--

[1] Percent occurrence refers to left and right sides combined.

TABLE 2.—Summary of red pigment cells in larval tunas from Hawaiian waters, August-September 1967.

Species	Number larvae examined	Larvae with red pigment	Red pigment cells on posterior half of trunk					
			Dorsal edge		Mid-lateral line		Ventral edge	
			Number[1]	Mean	Number[1]	Mean	Number[1]	Mean
Thunnus albacares	130	112	**0**, 1, 2, (3)	0.6	(0), 1, **2**, 3, 4, (5)	2.4	3-12	7.0
Thunnus obesus	63	47	**0**, 1, (2)	0.5	0, 1, **2**, 3, 4	1.9	1-8	5.3
Thunnus alalunga	6	6	**2**, **3**, (4)	2.6	(2), 3, **4**, (5)	3.5	5-12	8.0
Katsuwonus pelamis	138	88	**0**	0.0	**0**	0.0	1-12	7.2
Auxis spp.	72	51	**0**, (1)	0.0	**0**, 1, (2)	0.4	2-14	7.6
Euthynnus affinis	23	8	**0**	0.0	**0**, (2), (3)	0.3	4-10	6.7
Total	432	312						

[1] Less than 2% occurrence omitted.

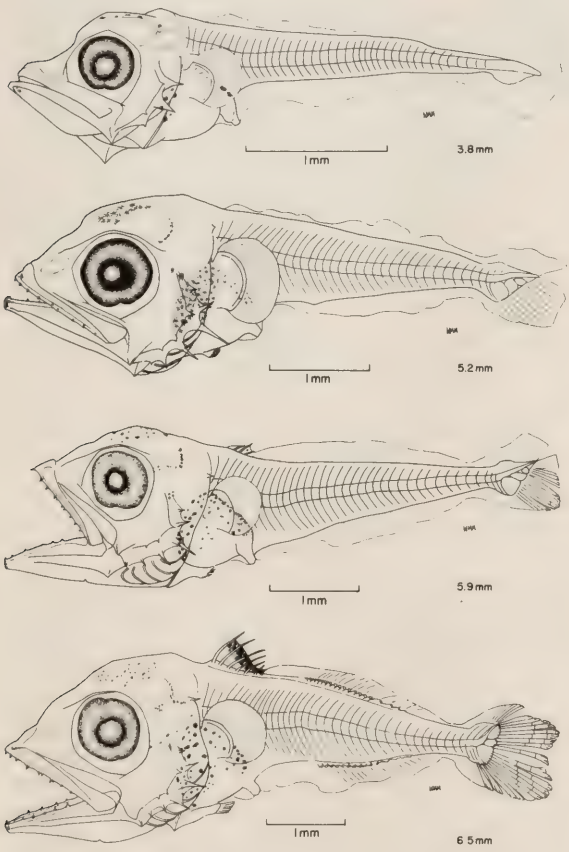

FIGURE 1.—Larval stages of *Thunnus albacares*, I. (From Matsumoto, 1958. Lengths have been converted from total to standard.)

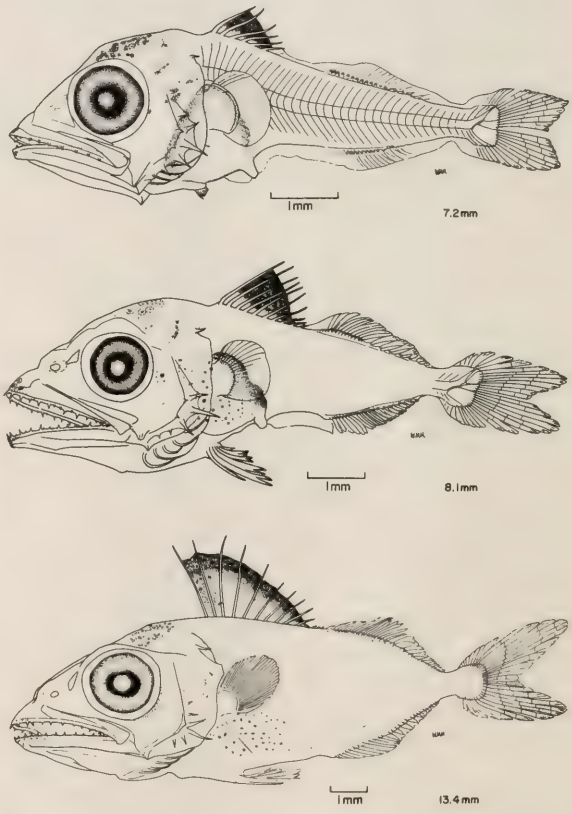

FIGURE 2.—Larval stages of *Thunnus albacares*, II. (From Matsumoto, 1958. Lengths have been converted from total to standard.)

first observed on the upper jaw tip in larvae about 5.0 mm SL and on the lower jaw tip at about 9.0 to 10.0 mm SL (Figures 3 and 4, reproduced from Ueyanagi, 1969). Consequently, all larvae between 4.5 and 7.0 mm SL having black pigment cells only on the lower jaw tip, and larvae between 7.0 and 9.0 mm SL having black pigment cells on the tips of both jaws were considered as *T. albacares*. All larvae between 5.0 and 9.0 mm SL having black pigment cells

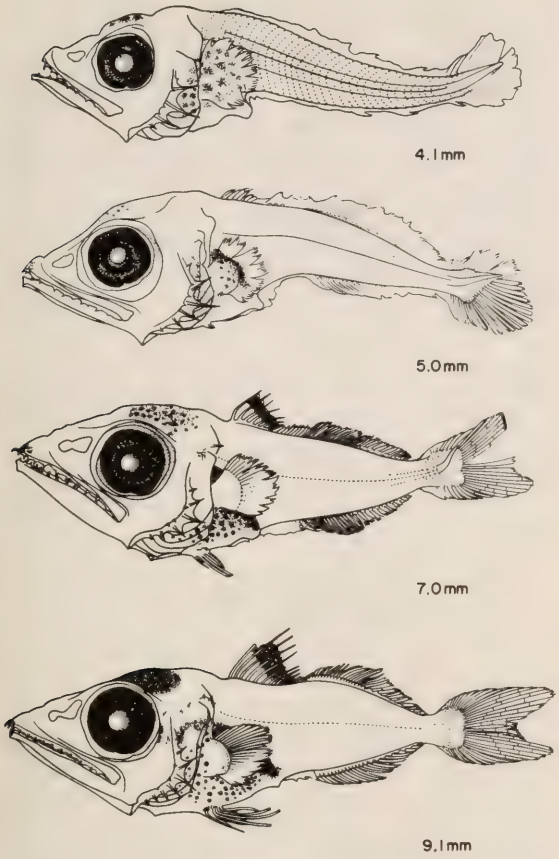

FIGURE 3.—Larval stages of *Thunnus alalunga*, I. (From Ueyanagi, 1969. Lengths have been converted from total to standard.)

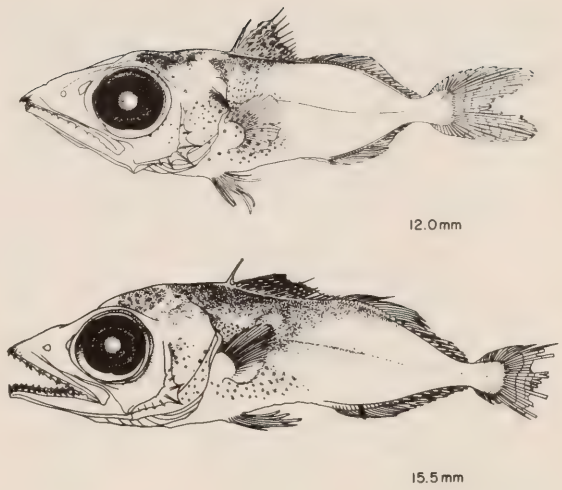

FIGURE 4.—Larval stages of *Thunnus alalunga*, II. (From Ueyanagi, 1969. Lengths have been converted from total to standard.)

only on the upper jaw tip were considered as *T. alalunga*. Larvae of the two species from 9.0 to 10.8 mm SL were separated by the position of black pigment cells on the lower jaw tip: in *T. albacares* the pigment cells were located on the inner, and sometimes outer, margins in larvae up to 10.8 mm SL, but in *T. alalunga* they were found only on the outer margin. It is suspected that the black pigment cells on the inner margin of the jaw in *T. albacares* migrate to the outer margin with further growth of the larvae.

Red pigmentation was accepted as a good supplementary character for separating *T. albacares* from *T. alalunga* (Tables 1 and 2). The distinctive patterns were located along the dorsal margin of the trunk from about the midpoint of the second dorsal fin base to the caudal peduncle. In *T. albacares* there was usually none or one red pigment cell at the caudal peduncle. Two pigment cells occurred seldom and three or four pigment cells occurred only rarely. Generally, these pigment cells were clustered at the caudal peduncle region. In *T. alalunga* there were usually two or three pigment cells, sometimes as many as four. Unlike those in *T. albacares*, these pigment cells were well spaced, extending forward to the middle of the second dorsal fin base. Only minor differences were noted in the red pigment cells along the mid-lateral line.

In larger larvae (10-13 mm SL) differences in the two species were noted in the distribution of pterygiophores of the second dorsal fin on cleared and stained specimens (Table 3). In *T. albacares* the two successive single pterygiophores between two adjoining neural spines occurred at the posterior end, whereas in *T. alalunga* they were at the anterior end. Additionally, the first haemal arch was on the 11th vertebra in *T. albacares* and on the 10th vertebra in *T. alalunga*.

TABLE 3.—Characters to separate larvae of *Thunnus albacares* and *Thunnus alalunga*.

Characters	*T. albacares*	*T. alalunga*
Small larvae (4-10 mm SL):		
Black pigmentation:		
Upper jaw	Appears at about 5.8 mm SL, mostly after 6.0 mm SL	Appears at about 5.0 mm SL
Lower jaw	Appears at 4.5-6.0 mm SL	Appears at 9-10 mm SL
	At tip on inner edge; migrate to outer edge with further growth	At tip on outer edge
Red pigmentation:		
Dorsal edge body, postanus	**0**, 1, 2, (3) [mean = 0.6]; near caudal peduncle	**2**, **3**, (4) [mean = 2.6] from peduncle to mid-second dorsal fin base
Lateral line, postanus	(0), **1**, **2**, 3, 4, (5) [mean = 2.4]	(2), **3**, **4**, (5) [mean = 3.5]
Ventral edge body, postanus	3-12 [mean = 7.0]	5-12 [mean = 8.0]
Large larvae (>10 mm SL):		
Array of [1]D_2 pterygiophores between two adjacent neural spines	1, 2, 2, 2, 3, 2, 1, 1	1, 1, 2, 2, 2, 3, 2, 1
Position of first haemal arch (vertebra number)	11th	10th

[1] D_2 refers to second dorsal fin.

Other *Thunnus* species

These species, which include *T. thynnus* (*T. thynnus thynnus* of Atlantic and *T. thynnus orientalis* of Pacific), *T. tonggol*, *T. maccoyii*, and *T. obesus*, have been identified mainly by black pigmentation on the trunk other than that over the abdominal wall.

In small *T. thynnus* of both Atlantic and Pacific Oceans (larvae between 3 and 10 mm SL), one or two large black pigment cells are present on the dorsal edge of the trunk between the second dorsal and caudal fins (Table 4, Figures 5 and 6), the anterior one usually being the larger. There may also be one to four black pigment cells on the ventral edge of the trunk between the anus and the caudal fin. Black pigmentation in *T. thynnus* from both oceans agrees quite well, except that in 5 out of 10 Atlantic specimens one or two tiny black pigment cells were noted along the mid-lateral line of the body near the pectoral fin, and in two instances a single tiny black pigment cell was found on the mid-lateral line beneath the posterior end of the second dorsal fin. These pigment cells were not considered reliable for identification purposes.

Observation of red pigmentation on larvae of Atlantic and Pacific *T. thynnus* is incomplete. Only one Atlantic *T. thynnus* larvae was examined for this character, but unfortunately the specimen was taken in a day tow so that the pigmentation appeared as a continuous streak on both the dorsal and ventral edges of the trunk as well as on the ventral surface of the lower jaw. In Pacific *T. thynnus* there were one to five red pigment cells, usually three, on the dorsal edge of the trunk. The number of red pigment cells on the mid-lateral line and ventral edge of the trunk has not been recorded, but according to the lllustration by Ueyanagi (1966), the pigment pattern may be similar to that of *T. obesus*. On the basis of black and red pigmentation, the Atlantic and Pacific *T. thynnus* were not separable.

The identification of *T. tonggol*, based on size series of 4.2 to 7.3 mm, has yet to be confirmed. Following the description of the species by Matsumoto (1962), larvae similar to these having the anteriormost black pigment cell on the dorsal edge of the body ahead of the second dorsal fin origin have been found in 1963 in the mid-South Atlantic Ocean near Ascension Island. Confirmation of the species description requires the finding of adults within this area and the finding of additional larvae to extend the identified size range.

The identification of *T. maccoyii*, which was first described as having black pigment pattern similar to that of *T. thynnus* (Yabe, Ueyanagi, and Watanabe, 1966) and later as having the black pigment cells on the dorsal edge of the trunk reduced to pinpoints (Ueyanagi, 1969), also needs verification (see discussion on *T. thynnus*). The correspondence of published descriptions based on eight specimens and observations of larvae identified as this species were not conclusive.

T. obesus was easily separated from *T. thynnus* by the absence of black pigmentation on the bases of the anterior dorsal finlets. Sometimes a single small black pigment cell was present along the ventral edge of the trunk near the caudal peduncle, but more often one to three pig-

TABLE 4.—Characters used to separate larvae of *Thunnus* species having black pigmentation on trunk.

Characters	*Thunnus thynnus* (Atlantic)	*Thunnus thynnus* (Pacific)	*Thunnus tonggol*	*Thunnus maccoyii*	*Thunnus obesus*
Small larvae (3-10 mm SL):					
Number of black pigment cells:					
Upper jaw tip	No observation	Appears above 6 mm SL	No observation	Appears above 5 mm SL	Few spots above 5 mm SL
Lower jaw tip	2 on inner edge	2 on inner edge above 4 mm SL	No observation	Appears above 4 mm SL	0-2 on inner edge below 4 mm SL
Dorsal edge trunk	1 or 2	1 or 2	1, 2, or more	1 or 2, very small	None
Lateral line	0-2 near mid-trunk	None	None	0 or 1 near mid-trunk	None
Ventral edge trunk	1-4	2 or more	2 or more	1-3	1 or more
Number of red pigment cells:					
Dorsal edge trunk	Streak on caudal peduncle[1]	1-5, mostly 3	No observation	No observation	0, 1, (2)
Lateral line	Indistinct[1]	Number not available	No observation	No observation	0, 1, 2, 3, 4
Ventral edge trunk	Streak anus to caudal peduncle[1]	Number not available	No observation	No observation	1-8 [mean = 5.3]
Lower jaw ventral view	Streak along margin anterior half of jaw and midline[1]	2 well spaced on anterior half	No observation	No observation	1 on each side near tip
Large larvae (>10 mm SL):					
Array of [2]D_2 pterygiophores between two adjacent neural spines	1, 2, 2, 3, 2, 2, 1, 1	No observation	No observation	No observation	1, 2, 2, 2, 3, 2, 1, 1

[1] Only one larva taken in a day tow was examined.
[2] D_2 refers to second dorsal fin.

ment cells were present along the base of the posterior half of the anal fin. Red pigmentation did not differ from that in *T. albacares*.

In larger larvae (10-13 mm SL) the array of pterygiophores of the second dorsal fin between two adjacent neural spines was sufficient to separate *T. thynnus* from *T. obesus* and both species from *T. alalunga* (Tables 2 and 3). In *T. thynnus* the greatest number of pterygiophores (3) between two adjacent neural spines appeared in the fourth position in the array, whereas in *T. obesus* and *T. alalunga* it appeared in the fifth and sixth positions, respectively. *T. obesus* was not distinguishable from *T. albacares* by this character.

The identification of *T. atlanticus* was not resolved. No larvae from the distributional range of this species (tropical western Atlantic) have been found which are distinguishable from any of the species considered above. One of us (Richards) suspects that *T. atlanticus* larvae are very similar to larvae of *T. obesus*. This suspicion is based on the great abundance of larvae resembling those of *T. obesus* in this area, particularly at times and places where *T. obesus* adults are rarely found or absent. Further studies are needed.

SUMMARY OF LARVAL IDENTIFICATION

On the basis of the examination and discussion above, the workshop agreed that:

1. The description of *T. albacares* by Matsumoto (1958) was correct (see Figures 1 and 2), but that the "appearance of black pigmentation at the tip of the lower jaw at about 4.5 mm SL" should be included.

2. The description of *T. alalunga* by Yabe and Ueyanagi (1962) and illustrations by Ueyanagi (1969) were correct (see Figures 3 and 4), but that the lower size limit should be set at about 4.5 mm SL until further studies indicate more precisely the earlier appearance of black pigmentation at the tip of the lower jaw in *T. albacares*.

3. It is not possible to separate larvae of *T. albacares* from *T. alalunga* below 4.5 mm SL, prior to the appearance of black pigment cells at the tip of the lower jaw in *T. albacares*.

4. The description of *T. thynnus* by Yabe, Ueyanagi, and Watanabe (1966) was correct

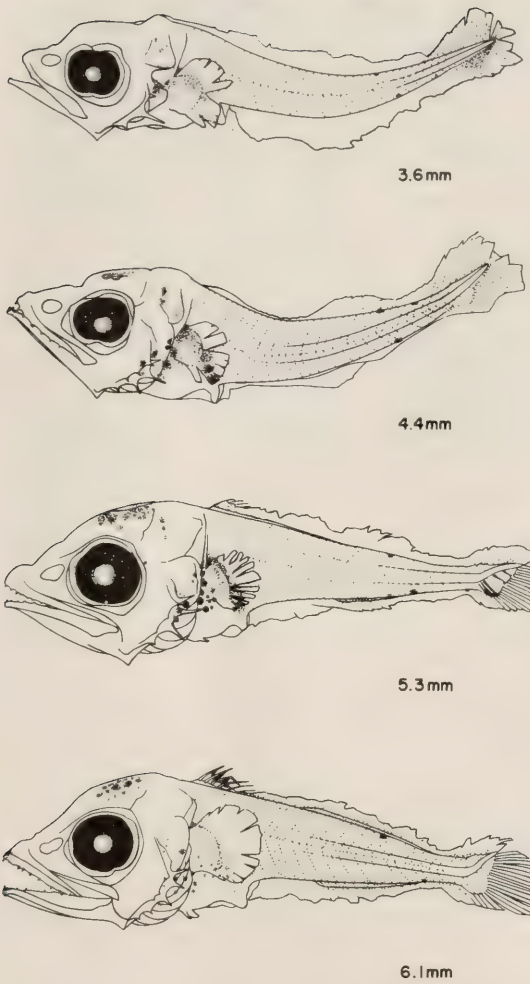

FIGURE 5.—Larval stages of *Thunnus thynnus*, I. (From Yabe, Ueyanagi, and Watanabe, 1966. Lengths have been converted from total to standard.)

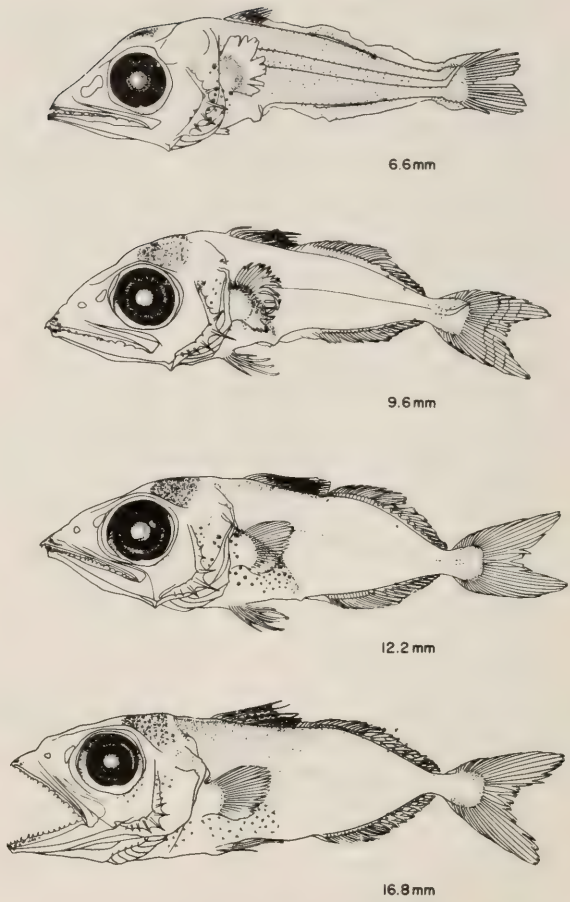

FIGURE 6.—Larval stages of *Thunnus thynnus*, II. (From Yabe, Ueyanagi, and Watanabe, 1966. Lengths have been converted from total to standard.)

(see Figures 5 and 6), and that there was no difference in *T. thynnus* from the Atlantic and Pacific Oceans.

5. The identification of *T. tonggol* was not substantiated by an adequate size series.

6. The description of *T. maccoyii*, based on tiny melanophores on the dorsal edge of the trunk, was not conclusive.

7. The description of *T. obesus* by Matsumoto (1962) was correct, though it needed to be augmented by illustrations of a complete size series.

8. The identity of *T. atlanticus* larvae is unresolved.

IDENTIFICATION OF JUVENILES

In spite of the intention of the workshop to assemble as many specimens of juvenile tunas as possible, only a few juveniles of *T. albacares* and *T. obesus*, not nearly enough to warrant their detailed examination, were available for study. The discussion on juvenile tuna identification, therefore, dealt mainly with published reports and with contributed data, resulting in a summary of identifying characters which the workshop considered useful and reliable.

Once the young tuna has acquired the full complement of spines and rays in all the fins, complete ossification of all the vertebrae, and the relocation of the anus near the origin of the anal fin, it is generally considered a juvenile of the species. Certain characters such as the full number of gill rakers, however, develop much later, when the juvenile has attained a length of 40 or 45 mm SL. If we consider juveniles to include all sizes up to the time of full gonad development signified by initial spawning, the size range of the juvenile stage would extend from about 13 mm SL to 700 mm FL (fork length) in *T. albacares* (Yuen and June, 1957) and to 860 mm FL in *T. alalunga* (Otsu and Hansen, 1962). For the purpose of clarifying species identification of the young, however, individuals beyond 200 mm SL need not be included. The term juvenile, as used here, thus refers to tunas between 13 and 200 mm SL.

EVALUATION OF CHARACTERS

The greatest difficulty in identifying juveniles of *Thunnus* is that the most useful characters are located internally. Except for the flattened first elongate haemal spine in *T. alalunga*, there is no single character that is peculiar to each of the species; but by using a combination of characters it should be possible to identify most of the other species. A summary of the most useful characters discussed is listed in Table 5. The size of juvenile at which each of the characters can be observed is listed also. Those characters whose usefulness in the early juvenile stages has not been shown conclusively are indicated by a question mark (?). The general formula of distribution of pterygiophores of the second dorsal fin has not been used before.

The counts and descriptions given for those characters listed with a question mark generally are those of the adults. These have not yet been substantiated for juveniles as well. Changes in the position of the first haemal arch with growth, for example, have been known to exist in other closely related fish such as the wahoo, *Acanthocybium solandri* (Matsumoto, 1967). This could be true of the tunas also.

Comparisons of body parts, particularly of orbit diameter, body depth at origins of the first dorsal and anal fins, preanal and postanal distances, and snout length, have not been investigated sufficiently in the past. The unavailability of specimens in sufficient numbers as well as the nonuniformity of body lengths (fork and standard) used have contributed greatly to this neglect. Acceptance of standard length as the standard measure of body length and publishing of actual measurements in the future should help in the accumulation of sufficient data for analyses. This has to be done by all workers in this field of study, since the juveniles are not easily taken in large numbers.

TABLE 5.—Characters for separating juveniles of *Thunnus* species.

Character	Useful on juveniles above	*Thunnus thynnus*	*Thunnus alalunga*	*Thunnus atlanticus*	*Thunnus obesus*	*Thunnus albacares*
First haemal arch	?	10	10	11	11	11
Ceratobranchial including angle	40 mm SL	17-20	15-16	12-13	15-16	15-16
Vertebrae	13 mm SL	18 + 21	18 + 21	19 + 20	18 + 21	18 + 21
Array of [1]D_2 pterygiophores between two adjacent neural spines	10 mm SL	1, 2, 2, 3, 2, 2, 1, 1	1, 1, 2, 2, 2, 3, 2, 1	1, 2, 2, 2, 3, 2, 1, 1	1, 2, 2, 2, 3, 2, 1, 1	1, 2, 2, 2, 3, 2, 1, 1
First prezygapophysis and position on haemal arch	?	15, 16, 17, high	15, 16, high	16, 17, low	15, 16, high	13, 14, low
Postzygapophysis near first prezygapophysis	?	Short, directed posterior	Short, directed posterior	Long, directed vertical or slightly anterior	Short, directed posterior	Long, directed vertical, some slightly anterior
First haemal spine	30 mm SL	Winglike at some stages	Extremely winglike	Winglike at some stages	--	--
Lateral line above base of pectoral fin	25 mm SL	Acute, nearly 90°	Obtuse	Obtuse	Obtuse	Obtuse

[1] D_2 refers to second dorsal fin.

DISCUSSION AND SUMMARY

T. thynnus below 25 mm SL can be separated from the other *Thunnus* species by the array of pterygiophores of the second dorsal fin, the last four positions containing 2, 2, 1, 1 pterygiophores; in *T. alalunga* the sequence is 2, 3, 2, 1, and in *T. atlanticus*, *T. obesus*, and *T. albacares* it is 3, 2, 1, 1. *T. thynnus* above 25 mm SL can be separated from all other *Thunnus* by the sharp angle (nearly 90°) which the lateral line follows near the base of the pectoral fin; in all other species this angle is obtuse. In juveniles above 40 to 45 mm SL, *T. thynnus* has the highest number of gill rakers on the ceratobranchial, including that at the angle (Potthoff and Richards, 1970).

T. alalunga below 30 mm SL can be separated from other *Thunnus* species by the distribution of pterygiophores of the second dorsal fin. Above 30 mm SL, *T. alalunga* is the only species whose first elongated haemal spine is flattened laterally and appears extremely winglike.

T. atlanticus as small as 13 mm SL can be separated from other *Thunnus* species by its distinctive precaudal and caudal vertebral counts. It is the only species having 19 precaudal and 20 caudal vertebrae. Above 40 to 45 mm SL, this species can be separated from the others by the low (12-13) gill raker count on the ceratobranchial (Potthoff and Richards, 1970), in addition to the vertebral formula.

T. obesus and *T. albacares* are the only two species that cannot be distinguished from each other on the basis of internal characters. Comparisons of body parts, i.e., orbit diameter, body depth or preanal and postanal distances, may have to be used.

ACKNOWLEDGMENTS

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THE FERTILIZATION OF GREAT CENTRAL LAKE. I. EFFECT OF PRIMARY PRODUCTION

T. R. Parsons,[1] K. Stephens,[2] and M. Takahashi[1]

ABSTRACT

Commercial fertilizer was added at a rate of 5 tons per week to a lake (51 km^2, mean depth 200 m) over a period of 5 months from May to October 1970. As a result of these additions, surface primary production was increased approximately tenfold while the primary production of the euphotic zone was doubled. The standing stock of primary producers and water clarity were substantially the same as in the previous year when no fertilizer was added. The productive index (mg C/mg Chl *a*/hr) was increased, especially in the immediate area of nutrient enrichment. However, the principal phytoplankton species were very similar at locations near and distant from the area of fertilization. In conclusion, it appears that as a result of adding nutrients at a low but sustained level, primary productivity was increased without substantially changing the nature of the food chain at the primary level of production.

In the Pacific northwest, an earlier study (Nelson and Edmondson, 1955) on the fertilization of a small salmon-producing lake in Alaska showed that the addition of phosphate and nitrate fertilizer increased the production of sockeye salmon (*Oncorhynchus nerka*); in more recent studies by Donaldson et al. (1968), an increase in the production of steelhead trout (*Salmo gairdneri*) was demonstrated in a small lake in the state of Washington. The natural fertilization of lakes from decomposing salmon carcasses has been discussed by Krokhin (1967), who has suggested that the potential deficit from salmon removed by the fishery should be replaced by artificial fertilization. In the report presented here we have carried out a fertilization experiment which differs from the two previous reports (Nelson and Edmondson, 1955; Donaldson et al., 1968) in several respects. These include the size scale of the experiment which was very much larger than any previous experiments, the application of fertilizer as a solution, control of the N:P ratio, and, finally, sustained weekly nutrient additions over a period of 5 months.

Preliminary results of our experiment have been reported (Parsons et al., in press) together with our conclusion that lake production was increased by the addition of fertilizer and that this was achieved without causing a condition of eutrophication. The following account deals specifically with the effect of nutrient enrichment on the primary level of production. Intensive studies on the effect of nutrient additions were carried out during the period May to August 1970 while a more general monitor program has been maintained from 1969 to the present (March 1971). The first sustained nutrient additions were made during the period June to October 1970 and further additions are planned for the next 5 years.

The primary purpose in this study is to increase levels of production in an oligotrophic lake, but not to change the trophic relationships which lead to the production of young sockeye salmon. In this respect the ultimate desideratum of the experiment is to produce larger sockeye smolts at their time of seaward migration; earlier reports have demonstrated that there is a close positive relationship between smolt size and survival (Ruggles, 1965; Johnson, 1965). Since previous studies (Parsons et al., in press) have shown that the migrant smolts from Great Central Lake are small (63 ± 1 mm) and that the primary productivity is very low (ca. 5 g

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$C/m^2/year$), application of nutrients at a level that would increase primary and secondary production seemed reasonable.

Data used in this presentation have been obtained from Stephens et al. (1969[3]) and Kennedy et al. (1971[4]).

METHODS

ANALYTICAL PROCEDURES

Chlorophyll *a*, nutrients, oxygen, and total CO_2 were all measured as described previously (Strickland and Parsons, 1968); bacteria were enumerated from plate counts after 24 hr incubation at room temperature on Millipore universal medium; major phytoplankton species were enumerated after settling preserved samples; conductivity was measured using a Beckman Solu Bridge (Cedar Grove, N.J.). Primary productivity was measured as the difference in uptake of $^{14}CO_2$ in light and dark bottles; however, on a few days the dark-bottle uptake was exceptionally high and this requires further investigation. For the purpose of this presentation, data have been used only for days when the dark-bottle uptake was less than 20% of the maximum light-bottle uptake.

Radiation was measured with an Epply pyranometer and corrected to give photosynthetically available radiation (PAR) as described previously (Parsons and Anderson, 1970). Light attenuation was routinely measured with a Secchi disc (SD), and an empirical relationship between SD depth (m) and the vertical extinction coefficient was established using a Schüler meter (maximum response at 430 nm). This relationship for light at 430 nm was:

$$K_{10}^{430} = \frac{2.1}{\text{SD depth}}$$

The (total) extinction coefficient for the water column was then found from Jerlov's (1957) light attenuation curves. Mean radiation (I_m) for the water column of depth (d_m) was determined from the expression

$$I_m = \frac{I_0\,(1-e^{-kd_m})}{d_m k}$$

where I_0 was the surface radiation and k was the attenuation coefficient for light below the surface meter. The expression was also used to determine the light at various depths in relation to the photosynthetic activity at those depths.

NUTRIENT ADDITIONS

The choice of a suitable fertilizer for the waters of Great Central Lake has been discussed previously (Parsons et al., in press). The nutrient addition consisted of a commercial grade of ammonium phosphate and ammonium nitrate which contained trace quantities of other elements essential for plant growth. The mixture is known commercially as 27-14-0 (27% N; 14% P_2O_5; 0% K_2O) and has an N:P ratio of 10:1.

The ammonium nitrate and ammonium phosphate were dissolved separately in 5-ton amounts (total) and the concentrated solutions mixed before distribution. A small quantity of organic material was added to the dissolved inorganic fertilizer at a dilution of 6 liters of fish solubles (obtained from B.C. Packers Ltd.) for every 2 tons of nutrient solution. The dissolved fertilizer was distributed at 10 gal/min (38 liters/min) in the wake of a vessel travelling at approximately 8 knots. The area of nutrient additions is shown in Figure 1, together with sampling stations 1, 2, and 3. Station 1 was sampled during 1969 and 1970, Station 2 was sampled during 1970, and Station 3 was sampled sporadically during 1970 in order to check on the flow of nutrients in a westerly direction; in addition, areal surveys for chlorophyll *a*, transparency, and bacteria were carried out over the whole lake in order to determine within-lake variation.

The area over which nutrients were added represented ca. 3 sq mi (8 km^2) of lake surface; however, from studies on lake circulation it was apparent that the material was transported east

[3] Stephens, K., R. Neuman, and S. Sheehan. 1969. Chemical and physical limnological observations, Babine Lake, British Columbia, 1963 and 1969, and Great Central Lake, British Columbia, 1969. Fish. Res. Board Can., Manuscr. Rep. 1065: 41-52.

[4] Kennedy, O. D., K. Stephens, R. J. LeBrasseur, T. R. Parsons, and M. Takahashi. 1971. Primary and secondary production data for Great Central Lake, B.C., 1970. Fish. Res. Board Can., Manuscr. Rep. 1127. 379p.

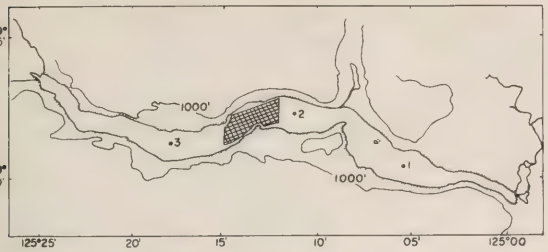

FIGURE 1.—Great Central Lake showing principal sampling stations (1, 2, and 3) and area of nutrient enrichment (crosshatched).

and west at rates of up to 6 miles per day or ca. 10 km/day (Parsons et al., in press). Thus while Station 2 was generally under the most immediate influence of the nutrient additions, Stations 1 and 3 also received an accumulative enrichment. Fertilizer was added at the rate of 5 tons per week from June through to October 1970. During May 1970 approximately 2 tons of fertilizer were added in experiments to determine the rate of mixing and distribution of nutrients in the vessel's wake.

RESULTS

LAKE MORPHOMETRY

Great Central Lake is located on Vancouver Island, B.C., at lat 49°20′ N on an east/west axis between long 125°00′ W and 125°25′ W (Figure 1). It is a long narrow lake (ca. 33 × 1.5 km) with steep sides and a mean depth of 200 m. The yearly mean discharge is approximately 6 × $10^6 m^3$/day with a range from 0.4 × 10^6 to 32 × $10^6 m^3$/day.

TEMPERATURE

The temperature structure at Station 1 is shown in Figure 2. The results are representative for the open waters of the whole lake, and it is apparent that the lake was isothermal during January and February; a thermocline started to form during March and was well established by May. Maximum surface temperature during July was 21.2° C; surface cooling started in September but a thermocline of

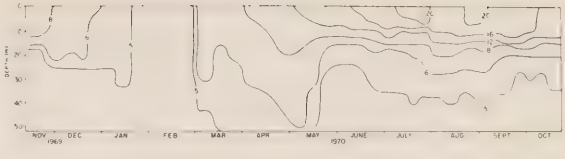

FIGURE 2.—Temperature (°C) stratification at Station 1.

10° persisted through October and the lake did not become isothermal until January of the following year.

RADIATION

Changes in photosynthetically active radiation (PAR) at the lake surface are shown in Figure 3 together with the mean radiation for the water column 0 to 20 m, calculated on a 24-hr basis.

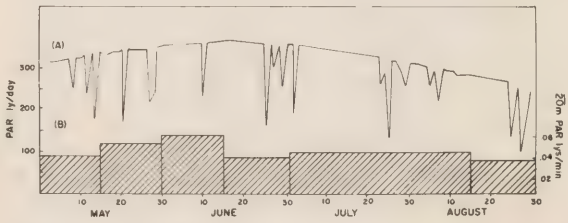

FIGURE 3.—(A) Surface photosynthetically active radiation (PAR) and (B) 15-day mean PAR in the first 20 m.

From the latter results it is apparent that radiation in the water column increased by 50% from the beginning of May until the middle of June; the decrease in radiation during the second part of June was due to a combination of higher extinction coefficients and lower surface radiation. The average radiation remained virtually constant during July and decreased by 20% during the latter half of August.

CHLOROPHYLL *A*

Surface chlorophyll *a* concentrations are presented in Figure 5 in the same way and for the same stations and years as SD data in Figure 4. The two figures have some mirrored similarities;

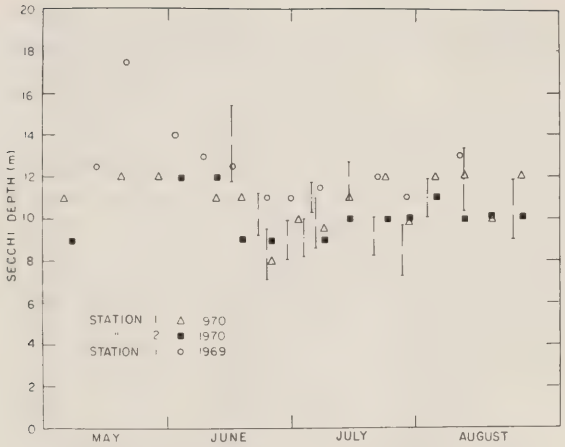

FIGURE 4.—Secchi disc depth at Stations 1 and 2, 1970, and Station 1, 1969. (Mean and standard deviation of values from areal surveys shown as bars.)

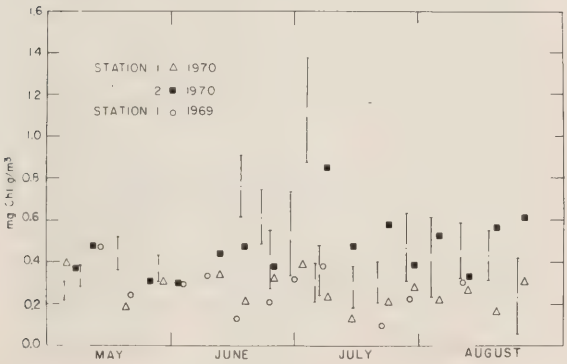

FIGURE 5.—Surface chlorophyll *a* data at Stations 1 and 2, 1970, and Station 1, 1969. (Mean and standard deviation of values from areal surveys shown as bars.)

thus Station 2 chlorophyll *a* values from June to August were generally higher than either Station 1 data for 1969 or 1970; minimum mean SD data (8 to 10 m) occurred between June and July during a maximum in the mean chlorophyll *a* concentration. However, 1969 chlorophyll *a* data at Station 1 do not appear to be significantly different from 1970 chlorophyll *a* data at the same station.

The depth distribution of chlorophyll *a* generally showed a maximum between 10 and 20 m following stratification and nutrient depletion in the surface layers.

pH, CALCIUM, TOTAL CO_2, AND CONDUCTIVITY

pH values were generally between 7.1 and 8.3 with some indication of a seasonal cycle towards higher pH values in summer. Several assays for calcium showed a concentration of 5 mg/liter while specific conductivity was very consistent at 33 μ mhos/cm, except in the immediate vicinity of small streams entering the lake; total carbon dioxide varied over a range from about 2.2 to 4.2 mg C/liter.

OXYGEN

Oxygen profiles to 200 m showed that surface oxygen concentrations were between 80 and 90% saturation during winter and up to 110% saturation during summer. Deepwater oxygen concentrations appeared constant at around 10 mg/liter or about 80% saturation. An oxygen maximum occurred at ca. 20 m during the summer.

NITRATE, AMMONIA, PHOSPHATE, AND SILICATE

Nitrate depth profiles at Station 1 during May to October, 1969 and 1970, are shown in Figure 6. The general form of the two profiles is similar; thus a depletion in the winter level of nitrate (1.0 to 2.0 μg at./liter) becomes apparent towards the end of May and by the end of June about 1 μg at. NO_3N/liter has been removed from the water column, 0 to 10 m. During July and August nitrate in the first 10 to 15 m is close to the limit of detection, but there is a partial return to winter levels during September and October. Some difference in the form of these events is apparent between 1969 and 1970; the utilization of nitrate was more rapid and apparently more complete during 1970; in addition, surface nitrates did not increase in September-October 1970 as they did in 1969.

Starting from a winter level of 2 μg at. NO_3-N/liter, the total utilization of nitrate in the water column has been determined for the periods February to May, June, and July-August using data shown in Figure 7. The accumulative amount

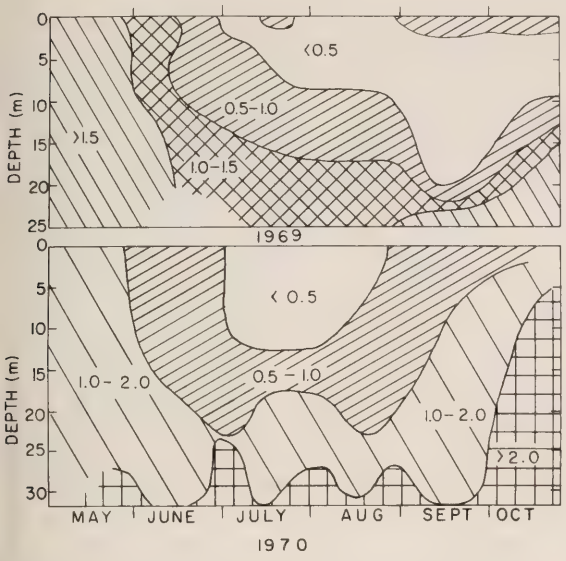

FIGURE 6.—Nitrate (μg at./liter) profiles at Station 1, May to October 1969 and 1970.

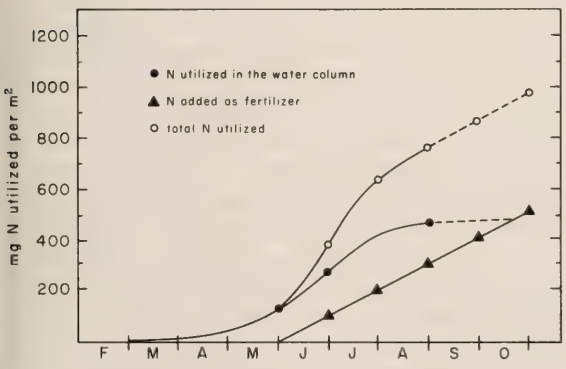

FIGURE 7.—N utilization at Station 1.

of inorganic nitrogen added as fertilizer (expressed per m^2 for the entire 51 km^2 lake surface) is also shown; since this was utilized within hours following each addition, the total nitrogen budget is represented as the sum of the natural and added inorganic nitrogen. Some mixing occurred during September and October, and the utilization of inorganic N during this period is shown as an indefinite extrapolation of the nitrogen utilized by the end of August. From these curves and Figure 5 it may be seen that the fertilizer was the principal source of new nitrogen during the period July-August when the lake nitrate was practically exhausted in the euphotic zone.

Ammonia values tended to show sporadic increases during 1970, and at times ammonia may have been the principal inorganic form of nitrogen in the lake, probably through being recycled as excretory products of the zooplankton (Beers, 1962). However, due to analytical difficulties with this radical, further investigation of its seasonal behavior is required, especially with reference to the verification of high values. Phosphate showed similar variations to nitrate although the depletion of phosphate was less regular. Seasonal concentrations ranged from <0.01 to 0.04 μg at. P/liter with about 3% of the values falling in a much higher range of 0.1 to 0.6 μg at./liter. A determination of phosphate utilized and phosphate added (similar to the inorganic N budget shown in Figure 7) was difficult to describe because of the unpredictable occurrence of phosphate throughout the summer; this may have been due to phosphate regeneration. As an overall assessment, however, if a winter level of 0.03 μg at. P/liter were completely utilized in the water column 0 to 30 m, the addition of 100 tons of 27-14-0 would increase the supply of phosphate over the whole lake by a factor of about 450% compared with the increase in the inorganic nitrogen budget of approximately 100% (Figure 7).

From winter to summer, silicate concentrations ranged from about 1.8 to 3.0 mg silica/liter. According to Lund (1965) silicate becomes rate limiting for diatoms at about 0.5 mg/liter, which is considerably lower than the seasonal range for Great Central Lake.

BACTERIA

Plate counts of bacterial colonies per 100 ml are shown in Figure 8, together with the range of counts obtained on several days when areal surveys were made. During May, the total number of colonies per 100 ml was generally below the mean value of ca. 9,000 reported by Henrici (1940) for oligotrophic lakes; however, there is

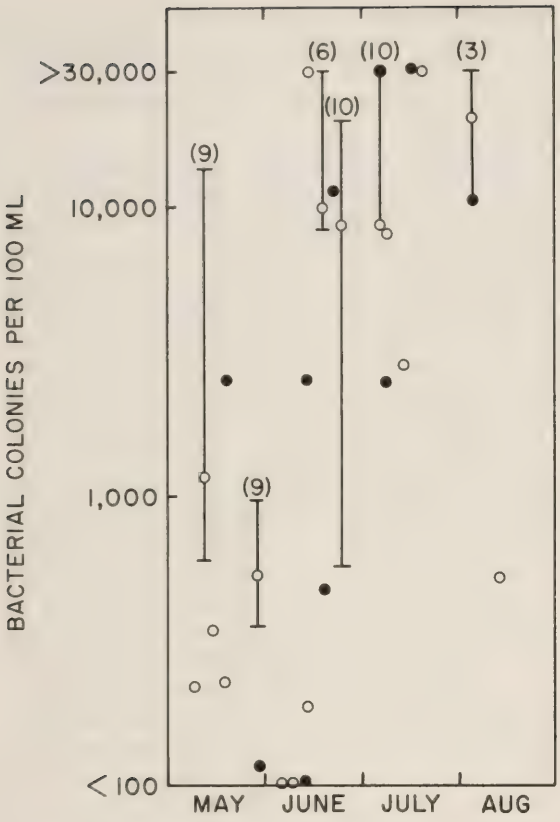

FIGURE 8.—Bacterial colonies per 100 ml surface lake water (○) Station 2; (●) Station 1; (5) number of samples in areal survey and range, I.

some indication in the data that bacterial numbers increased by one or two orders of magnitude during the latter part of June through to August. Summer increases in bacterial flora have been widely observed in lakes (e.g., Snow and Fred, 1926; Nauwerck, 1963), and while nutrient level could have affected this increase (e.g., see Bosset, 1965), we have no previous data on which to judge the effect.

PHYTOPLANKTON SPECIES

Principal phytoplankton species from surface samples at Station 1 and 2 during 1970 are shown in Figure 9 on a relative scale. From these results it is apparent that the predominant algae during May and early June were *Dinobryon, Rhizosolenia,* and *Nitzschia.* During June and July *Gymnodinium, Cyclotella,* and the euglenoid *Phacus* reached maximum numbers but tended to decline by August. Predominant algae of late summer and autumn were the chlorophyte *Nannochloris* and the cyanophyte *Chroococcus.* Second maxima in *Dinobryon, Rhizosolenia,* and *Cyclotella* occurred during the winter together with a maximum in *Tabellaria.*

Two studies (May and June) on the depth distribution of the principal species showed that maxima in *Rhizosolenia, Tabellaria,* and *Phacus* were found at the bottom of the thermocline (ca. 20 m); *Cyclotella* and *Gymnodinium* maxima occurred at the top of the thermocline (ca. 10 m) while *Nannochloris, Dinobryon, Nitzschia,* and *Chroococcus* showed maxima within the top 0 to 10 m.

PRIMARY PRODUCTION

Surface primary production values at Station 1 during 1969 and 1970 and at Station 2 during 1970 are shown in Figure 10; the mean and coefficient of variation of surface primary production for the months of June to August are also shown on each figure. The total average primary production in the water column 0 to 30 m at Stations 1 and 2 during 1970 was approximately 12 g C/m^2/year compared with approximately 6 g C/m^2/year at Station 1 during 1969.

Primary production per unit of chlorophyll *a* at different depths for Station 1, 1969 and 1970, and Station 2, 1970, are shown plotted against the light intensity at the same depths in Figure 11. A considerable amount of scatter is apparent in the data which is partly due to differences in environmental factors as well as to the lack of precision in attempting to establish photosynthesis versus light intensity relationships on the basis of ecological rather than experimental data. Polynomial curves were fitted to each set of data using an IBM computer. The shape of these curves is consistent with P vs. I relationships obtained by physiologists under experimental laboratory conditions and differences in asymptotic values reflect differences in the nutrient supply (Ichimura and Aruga, 1964).

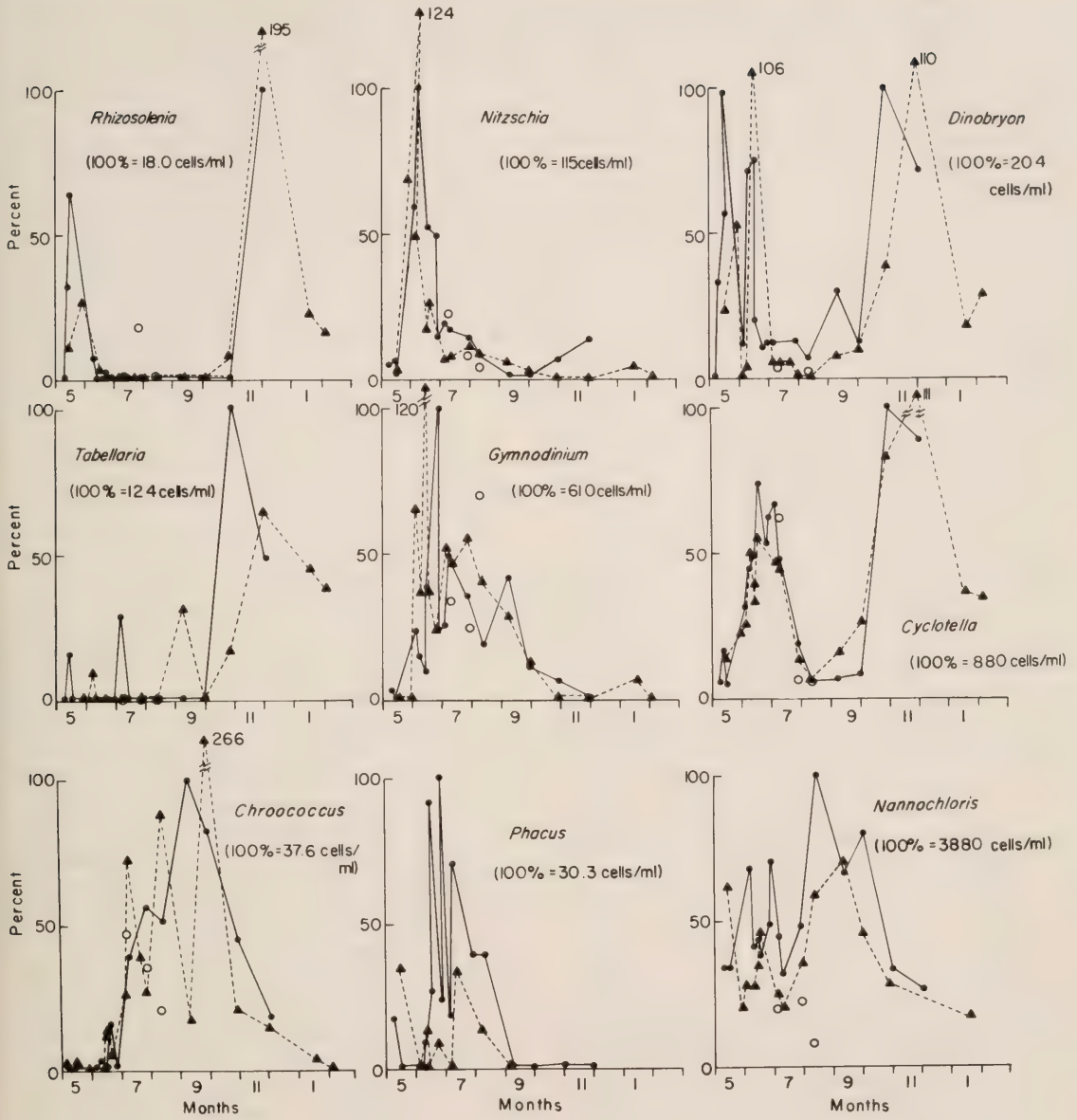

FIGURE 9.—Principal phytoplankton species at Station 1 (●), Station 2 (▲), Station 3 (○) during 1970.

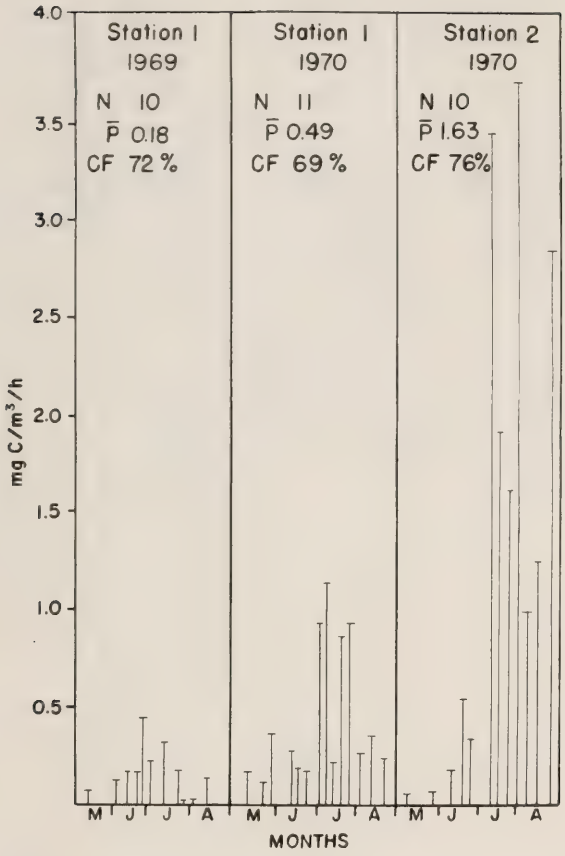

FIGURE 10.—Surface primary production, May to August. (N = number of samples, $\bar{P}$ = mean surface production, and CF = coefficient of variation—all values for the period, June to August.)

However the degree of scatter in the ecological data requires some expression of confidence limits. At Station 1 (1969), which was located at a considerable distance from the area of fertilization, 95% confidence limits for the asymptotic value of 1.03 mg C/mg Chl *a*/hr were 0.84 and 1.22; for 1970 at the same station the 95% confidence limits for the asymptotic value of 1.55

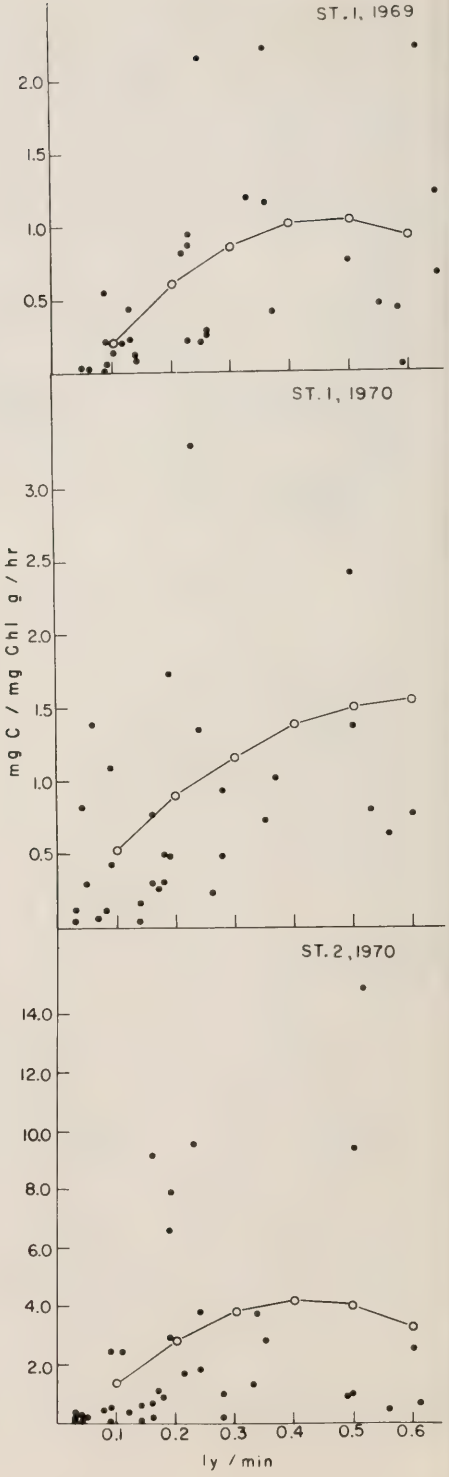

FIGURE 11.—Productivity indices plotted against light intensity at Station 1, 1969 and 1970, and Station 2, 1970 (○——○ computed best fitting polynomial curve).

mg C/mg Chl *a*/hr were 1.12 and 1.98. At Station 2 in 1970, however, the scatter of points is so great that 95% confidence limits become very large. The probable reason for this is that the station was sometimes in the area to which nutrients were first added, and sometimes the movement of water containing freshly added nutrients was away from Station 2 (Figure 1). If in fact it is assumed that there were only two alternatives in such a narrow lake (i.e., movement of nutrients towards or away from Station 2) then the 50% confidence limits for the asymptotic value of 4.17 mg C/mg Chl *a*/hr were 2.26 and 6.07.

DISCUSSION

The principal purpose of this report is to establish the effect of inorganic nutrient enrichment on the primary production of Great Central Lake. From data in Figure 10 it is quite apparent that primary productivity was increased in surface samples during 1970 compared with 1969, both at Station 1 and particularly at Station 2, which was very close to the area of repeated enrichment. However, while the effect of nutrient enrichment was apparent to the extent of a tenfold increase in surface primary productivity, the integrated productivity for the water column only showed an approximate doubling in primary productivity during the first 3 months of nutrient enrichment (see Parsons et al., in press, for primary production depth profiles). This result is in keeping with the fact that the total inorganic nitrogen addition to the lake (Figure 7) was only sufficient to approximately double the natural reservoir of inorganic nitrogen in the upper 10 m, based on winter nitrate levels. However, it does not take into account nitrogen fixation by the blue-green alga, *Chroococcus*, which may have taken arvantage of the increased supply of phosphate to become one of the predominant summer plankters.

The question is, whether some factor other than fertilization could have accounted for the increased primary productivity? Firstly, it is apparent that since the largest increase in primary productivity occurred at the surface, it cannot be argued that the increased primary productivity was due to greater enrichment of the water column from the hypolimnion, especially in view of the high degree of stratification (Figure 3) and apparent nitrate depletion in the epilimnion (Figure 6). It might be argued that the increased productivity was due to an increase in standing stock of primary producers and increased radiation. Data in Figure 5 indicate that the standing stock of primary producers at Station 2 was generally higher than at Station 1 during 1969, although the effect is within a 95% probability of being due to within-lake variations in standing stock of chlorophyll *a*. However, in order to examine this question in more detail, primary productivity data for Stations 1 and 2 in 1970 and Station 1 in 1969 have been expressed as the production per unit chlorophyll *a* and plotted against the calculated light intensity at various depths (Figure 11). This presentation of data has been used by Ichimura and Aruga (1964) to compare the productivity of oligotrophic, mesotrophic, and eutrophic lakes under conditions of different standing stocks of primary producers, light conditions, and photosynthesis. From their findings it was concluded that oligotrophic lakes had a productive index of between 0.1 and 1.0 mg C/mg Chl *a*/hr, which is very similar to the range of values computed from the data in Figure 11 for Station 1 during 1969. The computed range for Station 1 during 1970 was appreciably higher, however, and enters the classification for mesotrophic lakes which have a photosynthetic index of up to 2 mg C/mg Chl *a*/hr; finally the asymptotic value (4.17) from Station 2 in 1970 is within Ichimura's and Aruga's (1964) range for eutrophic lakes, which the authors report as having photosynthetic indices of up to 6 mg C/mg Chl *a*/hr. Since the only basis for this classification is the effect of nutrient enrichment in enhancing the photosynthetic response, it may be concluded that our observed increase in primary productivity was determined by the artificial addition of fertilizer.

Secondary effects of nutrient enrichment may also have influenced the primary formation of particulate material through a heterotrophic cycle. Unfortunately, our evidence for this is not substantial and rests mainly on the increase

in bacterial numbers (Figure 8) and the fact that very high dark uptake of ^{14}C-bicarbonate (up to 50% of the light bottle uptake) were encountered during the summer at some stations following fertilization. We are at present not sure of the accuracy of this result, however, and it will be reinvestigated during 1971. Nauwerck (1963) has concluded that the heterotrophic formation of particulate material is a principal mechanism for supplying food to particle feeders in some lakes and one might expect this mechanism to be enhanced by the additional availability of nitrogen and phosphorus.

The most interesting aspect of changes in the species composition of the principal primary producers is that in spite of differences in surface primary productivity at Stations 1 and 2 during 1970 (Figure 10) the relative abundance of principal species at these two stations (and on several occasions at Station 3) was substantially the same (Figure 9). This was important because it was intended that there should be no change in the species composition of organisms leading up the food chain to young salmon, but only an increase in their productivity. In addition, the occurrence of the *Cyclotella-Chroococcus* association is characteristic of oligotrophic lakes (Hutchinson, 1967) which indicates that the general classification of the lake (based on species association) had not been changed by fertilization. However, some eutrophic species of phytoplankton, such as *Ceratium, Peridinium,* and *Scenedesmus,* were also observed as minor constituents of the plankton, especially during the summer.

In conclusion, it appears that the fertilization of Great Central Lake resulted in an increased primary production but did not substantially change the standing stock of primary producers, water clarity, or the principal phytoplankton species at locations near and distant from the site of nutrient enrichment. The effect of zooplankton on the primary producers was essentially to suppress the increase in standing stock of phytoplankton while the standing stock of zooplankton itself increased by almost an order of magnitude. Zooplankton growth and distribution are described in the second paper in this series (LeBrasseur and Kennedy, 1972).

ACKNOWLEDGMENT

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THE FERTILIZATION OF GREAT CENTRAL LAKE
II. ZOOPLANKTON STANDING STOCK

R. J. LeBrasseur and O. D. Kennedy[1]

ABSTRACT

The regional, vertical, and seasonal abundance of the dominant zooplankton species were studied in conjunction with a series of nutrient additions to Great Central Lake. Two rotifer species, *Kellicottia* spp., *Conochilus unicornis*, three cladocera species, *Bosmina coregoni*, *Holopedium gibberum*, and *Daphnia longiremis*, and three copepod species, *Cyclops bicuspidatus thomasi*, *Epischura nevadensis*, and *Diaptomus oregonensis* were the most numerically abundant zooplankton species. The introduction of the fertilizer and the consequent higher rate of primary production produced no changes in the species composition. The zooplankton exhibited a relatively uniform horizontal distribution within the upper 20 m along the lake, a factor which was attributed to the lake circulation. All eight species were concentrated in the euphotic zone (upper 40 m), and five were most abundant in the upper 10 m. The center of abundance for the remaining three species was between 20 and 30 m depth. The respective depths of maximum abundance for the various species showed little variation between daylight and darkness. Seasonally, there were two periods, June to July and September to October, of maximum abundance for most species. The cause for somewhat lower levels of abundance in August is not known. The average zooplankton biomass showed a similar seasonal pattern with a maximum weight in July which exceeded 8 g/m^2. The average biomass over a 6-month period, May through October, exceeded 5 g/m^2 (more than 10 times greater than for the comparable period prior to fertilization in 1969). In contrast to the high standing stock of zooplankton, the estimated growth rate for underyearling sockeye salmon, the principal predator species in the lake, was only slightly improved over 1969 (1.2 vs. 0.9%/day). In comparison with other lakes producing young salmon the growth rates appear low with respect to the zooplankton stock. It was suggested that the temperature structure of the lake, 14° to 23°C above the thermocline and 4° to 6°C below the thermocline, may reduce availability and prevent the efficient utilization of the zooplankton by the underyearling sockeye salmon.

The following account is the second in a series of papers which report on the effects of sustained nutrient additions to an oligotrophic lake. In the first report, Parsons et al. (1972) showed that an increased primary productivity resulted from nutrient additions made to Great Central Lake, B.C.; the objective of this report is to determine if nutrient additions affected the standing stock and diversity of secondary producers.

The overall purpose of these studies has been to determine if nutrient additions will increase sockeye salmon (*Oncorhynchus nerka*) production; zooplankton, as the principal food of underyearling sockeye salmon, occupy a central position in the food chain of young sockeye during lake residence. Previous studies (Ivlev, 1961; Johnson, 1965; Brocksen et al., 1970) have suggested that prey density and availability may limit the predator biomass. The latter authors compiled data for several sockeye nursery lakes with which they were able to demonstrate a direct relationship between mean zooplankton biomass (prey) and the mean growth rate and biomass of underyearling sockeye salmon (predator). Other studies (Ricker, 1962) have indicated that the ocean survival, i.e. the return to coastal waters of adult sockeye salmon, can be directly correlated in many instances with the size at which the sockeye as year-old migrants leave the nursery lakes to enter the ocean for 2 or more years. While the above studies rely heavily upon circumstantial data, as well as data which were collected for other purposes, they serve as a rational basis for attempting to increase the available zooplankton biomass for the enhancement of salmon growth.

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METHODS

Sampling of zooplankton was initiated in mid-1969, using a 0.25 m^2 mouth area cylinder-cone net with 100 micron mesh aperture, hauled vertically from 20 m or 50 m. The samples were collected at infrequent intervals during 1969 and the first 14 weeks in 1970; thereafter vertical net hauls were made at two locations at least once every 4 days until the first week of November. Additional vertical net hauls were made once or twice each month from the lake bottom, 200 m, to the surface. Miller nets (Miller, 1961) with 0.01 m^2 mouth area and 100 micron mesh aperture were used at weekly intervals during the period June through August and thereafter at monthly intervals to determine the areal and vertical distribution of zooplankton. The areal sampling at 18 locations along the lake consisted of 5 min oblique tows from 20 m to the surface while underway at 2 m/sec. The daylight vertical distribution of zooplankton was monitored at 18 depths between the surface and 65 m by making three consecutive tows each with six Miller nets at 2 m/sec at one location. Additional tows were made to sample other depths and also at other periods of the day. Details of the sampling and sampling locations are reported elsewhere (Kennedy et al., 1971[2]).

In the analyses of samples special effort was made to maintain up to date species counts and measurements for comparison with other events as they were occurring in the lake. The common zooplankton constituents were identified, measured into size categories, and counted from an aliquot of the total sample; fractions of 1/50 or 1/100 using a Stempel pipette were used depending upon the sample size. The size categories (length in microns) reported in Table 1 were based upon individual measurements for different stages of development of the respective species. It is to be noted that the lengths refer to mean sizes of organisms during the spring and summer growing period. Individual length measurements for the different species and for different times of the year may be found in the MS data report (see footnote 2).

Species counts in vertical net hauls are reported as number per m^2, in oblique and horizontal tows as number per m^3. In this report, unless otherwise indicated, counts all refer to numbers of individuals which fall within the size range occupied by mature (Stage VI) copepods and egg-bearing cladocera; these were usually the two largest size groups for the species reported in Table 1.

RESULTS

SPECIES

Table 2 lists the species of zooplankton which have been found in Great Central Lake. Additional species may be present as minor constitu-

[2] Kennedy, O. D., K. Stephens, R. J. LeBrasseur, T. R. Parsons, and M. Takahashi. 1971. Primary and secondary productivity data for Great Central Lake, B.C., 1970. Fish. Res. Board Can., Manuscr. Rep. No. 1127, 379 p.

TABLE 1.—Zooplankton size ranges for species sorting in Great Central Lake.

Species	Group						
	I	II	III	IV	V	VI	VII
				Size range μ			
Cyclops bicuspidatus	Egg	125-275	375-550	550- 750	750- 850	850- 950	950-1,100
C. vernalis	Egg	275-375			750- 900	900-1,100	1,100-1,350
Epischura nevadensis	Egg	275-450	450-650	650- 900	900-1,100	1,100-1,350	1,350-2,250
Diaptomus oregonensis	Egg	125-275	450-750	750- 900	900-1,100	1,100-1,350	
D. kenai	Egg			650-1,100	1,100-1,750		1,750-2,500
Bosmina	Egg	125-225	225-325	325- 450	450- 650	650- 800	
Holopedium	Egg	375-450	450-750	750-1,100	1,100-1,750		
Daphnia longiremis	Egg	450-750	450-750	750-1,100	1,100-1,750		
D. pulex	Egg	450-650	450-750	750-1,100	1,100-1,750	1,750-2,500	
Kellicottia	Egg	ca. 80					
Conochilus	Egg	ca. 80					
Keratella	Egg	ca. 80					

TABLE 2.—Zooplankton species found in Great Central Lake, 1970.

Rotifera	Copepoda
**Kellicottia* spp.	**Cyclops bicuspidatus thomasi*
Keratella cochlearis	*C. vernalis*
K. quadrata	**Epischura nevadensis*
**Conochilus unicornis*	**Diaptomus oregonensis*
	D. kenai
Cladocera	**Unknown**
**Bosmina coregoni*	Actinopoda
**Holopedium gibberum*	Pollen
**Daphnia longiremis*	Egg clusters
D. pulex	Arachnoidea (mites—2 spp.)
Scapholeberis kingi	Chironomid larvae
Polyphemus pediculus	Fish larvae (cottid)
Alona affinis	

* Indicates the most common species.

ents of the zooplankton and it is also possible that new species are being introduced into the lake through a hydroelectric installation which discharges water from an adjacent watershed into the lake. It will be noted from Table 2 that the common zooplankton constituents consisted of two rotifer species, three species of cladocera, and three species of copepods; these species are identified throughout the text by their generic names. There has been no change in the species composition during the course of the experiment, i.e. the common species have remained numerically abundant while the rare species have continued to occupy a minor role.

PATCHINESS

It was anticipated that the zooplankton would exhibit contagious distributions reflecting local circulation patterns, species preferences, and predation. Accordingly, oblique samples from 20 m were collected at weekly intervals at 18 positions along the lake, both near the shore and in midlake. In general, with the exception of the area near the inlet and outlet of the lake where the abundance of organisms was sometimes low, there was greater variability found with respect to the date of sampling than the location of sampling. Weekly means and standard deviations computed for each species showed that *Cyclops* was the only species in which the standard deviation exceeded the weekly count for more than half the surveys (11 out of 17). The apparent variability in *Cyclops* abundance might be due contagion or, more likely, to the fact that sampling was limited to depths (20 m) where *Cyclops* were seldom abundant (see section on vertical distribution). The major source of variability in weekly mean counts appears to be associated with the number of organisms counted, i.e. the number of organisms in a sample and the size of the aliquot counted. The weekly mean number of organisms for each species were grouped together with their respective standard deviations as follows: 1-50, 51-250, 251-500, 501-1,000, 1,001-2,000, 2,001-5,000. The mean coefficient of variation (C.V.), the range, the number of means present in each group, and the number of times a standard deviation exceeded its respective mean are shown in Figure 1 (e.g. for 50 or fewer organisms counted, the standard deviation in 17 out of 23 samples exceeded the mean). The magnitude of C.V., or the relative variation about a mean, is closely associated with the number of organisms counted. The high degree of variability about a mean of 50 or fewer organisms reflects counting errors due to the subsampling technique used in the initial analyses of the samples. However, counts of organisms of 250 or more per m^3 tend

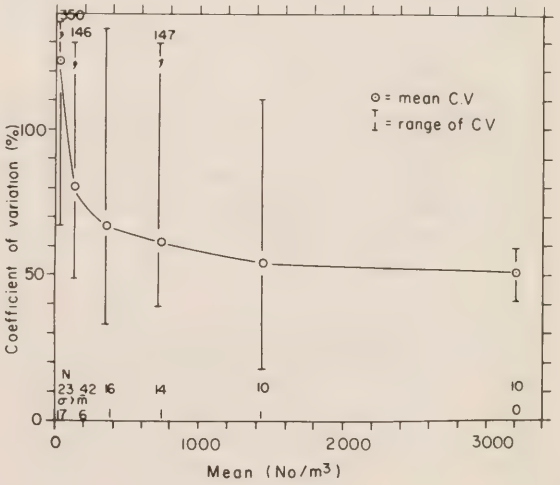


FIGURE 1.—Coefficient of variation computed for mean counts of species sampled in oblique (20 m to surface) tows, where N is the number of weekly means, $\bar{m}$ and σ is the standard deviation.

to be relatively uniform, suggesting that horizontal patchiness or local contagion is not a typical feature of Great Central Lake zooplankton. The observations of lake circulation (McAllister, personal communication) (Parsons et al., in press), and the chlorophyll *a* distribution (Parsons et al., 1972) confirm that the epilimnion is well mixed, thus assuring a nearly uniform dispersal of planktonic organisms along the lake.

The 50-m vertical hauls made at Stations 1 and 2 provide further opportunity for examining the variability with respect to different sampling locations. Here, the comparisons of *mean* counts indicated a high degree of similarity between the two locations with respect to species composition, stage of development, and abundance. However, examination of samples collected on the *same day* indicated a high degree of variability. Forty-nine samples were collected from Stations 1 and 2 during May through December; species counts for Station 1 were plotted against the respective count for Station 2. Values which fell outside of a mean $\pm$ half the expected mean (where the expected mean equals half the counts for Stations 1 and 2 combined) are tabulated in Table 3. On half the sampling dates the counts for a particular species tended to be similar at both locations (e.g. in the first column of Table 3, the number of samples with a mean $\pm\ m/2$ is generally greater than half the total number of samples, $N/2$). Greater numbers of four species were found at Station 2 than at Station 1. It is noteworthy that three of the four species, *Kellicottia*, *Cyclops*, and *Daphnia*, have their greatest abundance below the epilimnion at depths greater than that sampled on the areal surveys. However, there was no apparent correlation in the relative abundance of any of these three species with respect to each other or to other species at either station.

TABLE 3.—Comparison of counts of zooplankton from 50-m vertical hauls at Stations 1 and 2, $N = 49$.

Species	Counts $= (m \pm \frac{m}{2})$	Station 1 $>(m + \frac{m}{2})$	Station 2 $<(m - \frac{m}{2})$
Cyclops	33	5	11
Epischura	31	10	8
Diaptomus	24	10	15
Bosmina	26	17	6
Holopedium	25	15	9
Daphnia	22	6	21
Kellicottia	24	9	16
Conochilus	29	14	6

There were, however, periods when three or more species would be more abundant at one position than at the other. For example, from July 3 to July 21 (six sets of samples) three to six species were most abundant at Station 1 while during the period August 21 to September 8 (six sets of samples) three to seven species were most numerous at Station 2. Similarly, for other periods of 4 to 12 days, one or another species was in greater abundance at one station than the other.

These data have not been examined further to show if variation in species abundance between sampling positions can be correlated with variations in the lake circulation or other environmental factors such as fertilization or predation by underyearling sockeye. However, it is apparent that all seasonal changes in species composition and abundance were reflected throughout the near-surface waters of the lake and that no local area of high or low zooplankton concentration could be clearly defined within the main body of the lake.

VERTICAL DISTRIBUTION

Horizontal tows made within the upper 60 m revealed marked differences in species composition and abundance with depth during the period of thermal stratification. As an example the weekly tows made during July were combined and the average concentration of each species at each of 17 depths sampled during daylight is shown in Figure 2. The inset associated with each species distribution shows the relative distribution (25% quartile intervals) of the respective populations sampled during a 24-hr period in August.

Five of the eight species shown in Figure 2 have their maximum concentration within the upper 10 m, while the maximum concentration of the other three species was below 20 m. Thus the species maxima fall either above or below the thermocline. However, it should be noted that the number of organisms per m^3 decreased from a maximum of greater than 7,000/m^3 be-

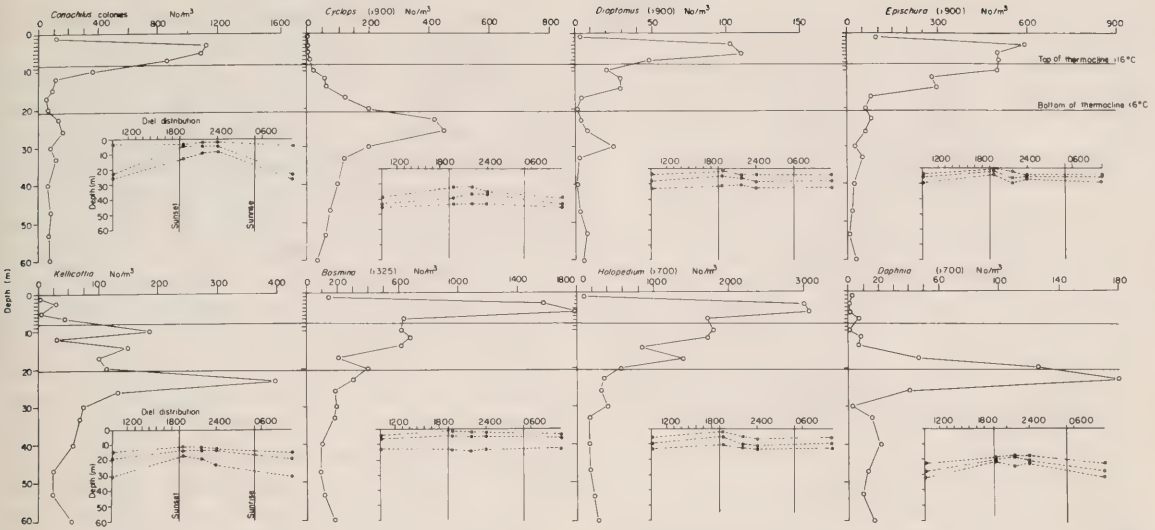


FIGURE 2.—Vertical distribution of common zooplankton species in Great Central Lake mean no./m³ for July 1970. (Horizontal lines indicates the top and bottom of the thermocline, McAllister (personal communication). Inset shows the vertical distribution at 25% quartile intervals over a 24-hr period. Note: the scale indicating the quantity of organisms varies for each species.)

tween 3 m and 5 m to a minimum of approximately 500/m³ at depths below 40 m. The maximum concentration of individual species ranged from 180/m³ for *Daphnia* to greater than 3,000/m³ for *Holopedium*. The tendency for some species to show an increase in abundance in deep samples was likely due to contamination from shallower depths since in the process of setting and hauling with nonclosing nets the deeper nets actually sample for a slightly longer time than the shallower nets. Variations in abundance with respect to time of sampling was noted for all species (Figure 2 inset). The effect was generally most pronounced just after sunset when the maximum concentration per m³ of a species might be increased by 30%. Rotifers, which were presumably the least motile of the zooplankton, exhibited the largest shift in abundance towards the surface with the onset of darkness. Some species, notably *Holopedium* and *Epischura*, returned to their daylight depth of maximum abundance within 2.5 hr after sunset. Other species, such as rotifers, *Bosmina*, and *Daphina* exhibited relatively little movement during darkness. It is apparent from Figure 2 that the shift in species abundance were all within the daylight range occupied by the bulk of the respective populations. Furthermore, more than 75% of the zooplankton populations were at all times within the euphotic zone (i.e. surface to 30-40 m).

SEASONAL ABUNDANCE

In Figure 3 the mean monthly numbers of zooplankton are shown for the 50-m vertical haul samples. Three species, *Cyclops*, *Bosmina*, and *Kellicottia*, were relatively abundant throughout the year, whereas the other species were present in numbers which exceeded 1,000/m² for periods of 4 to 5 months. *Conochilus* were the only species present during 1970 to appear subsequent to the initiation of nutrient addition. (They were present in 1969 samples.) *Cyclops* ranged from a winter minimum of 2,000/m² to a maximum in September and October of 30,000/m². *Epischura* were never numerically dominant but ranged in numbers from 2,000 to 4,000/m² from May through September. Counts of *Diaptomus* did not exceed 1,000/m² until August, but by September there was a

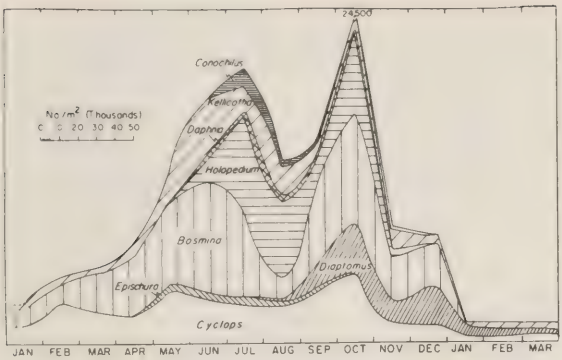


FIGURE 3.—Monthly mean zooplankton abundance (no./m² in the upper 50 m data from Stations 1 and 2 combined).

7-fold increase which in turn doubled to ca. 26,000/m² by October. The November-December catches of *Diaptomus* exceeded 10,000/m², which was approximately two orders of magnitude greater than their standing stock 12 months earlier. Substantial numbers of *Diaptomus*, 3,000 to 4,000/m², were carried through into 1971. *Bosmina* were the most abundant species collected throughout the year. Their numbers ranged from ca. 8,000/m² in January to ca. 60,000/m² in June and again in October. The December concentrations of *Bosmina* were twice that of the preceding January. However, by January of 1971 *Bosmina* had virtually disappeared from the water column, 0 to 50 m. *Holopedium* attained their maximum abundance in July, approximately 3 months after they began appearing in the samples in significant quantities, i.e. greater than 1,000/m². Following a secondary maximum in October, *Holopedium* were virtually absent from samples collected from December through March. *Daphnia* were the least numerous of the zooplankton species routinely sampled. They occurred in numbers of 1,000 to 3,000/m² from June through September. *Kellicottia* exceeded 10,000/m² from May through August and again in October and November. Nearly twice as many *Kellicottia* were present in December as were present at the beginning of 1970. The maximum abundance of *Conochilus* colonies (2,000/m²) was during July; no colonies were found prior to June and by December the number of colonies had declined to approximately 500/m².

In toto there were two to three times more zooplankton present in December of 1970 than there were the preceding January. It is of interest to note that the greater abundance of zooplankton at the end of 1970 was not maintained through the first 3 months of 1971 and further, that *Bosmina* had been apparently supplanted by *Diaptomus* in 1971. On a monthly basis there were fewer than 22,000 organisms/m² in January while in October, where the maximum concentration was observed, there were nearly 10 times as many organisms present. Zooplankton counts exceeded 100,000/m² in June, July, September, and October. The decrease in zooplankton abundance in August was approximately 15% lower than that in either July or September; this decline was attributable mainly to fewer numbers of *Bosmina*.

Individual species counts (4-day running mean number/m²) in vertical hauls have been presented in Figure 4 in order to show the seasonal variations in abundance in greater detail than is shown in Figure 3. The general features of both figures are the same but in Figure 4 the rapid increase and decrease in numbers of some species are shown more clearly, e.g. *Holopedium* and *Epischura*. From Figure 4 it is possible to infer some relationship between the addition of nutrients and the appearance of *Conochilus* or the sustained increase in the abundance of *Diaptomus*. It is noteworthy that all species, with the exception of *Epischura* and possibly *Daphnia*, went through a secondary maximum in October which was nearly as great as or greater than their level of abundance earlier in the summer.

SEX RATIO

Adult stages of *Cyclops* and *Epischura* showed marked imbalances from an expected 50:50 ratio of females to males through the year (Table 4). Males of these two species were clearly predominant during the late winter and early spring months. *Cyclops* females were predominant among the adults taken in June through August whereas *Epischura* females were never numerically dominant for more than two or three sampling periods, i.e. July 21 to 31, August 28 to

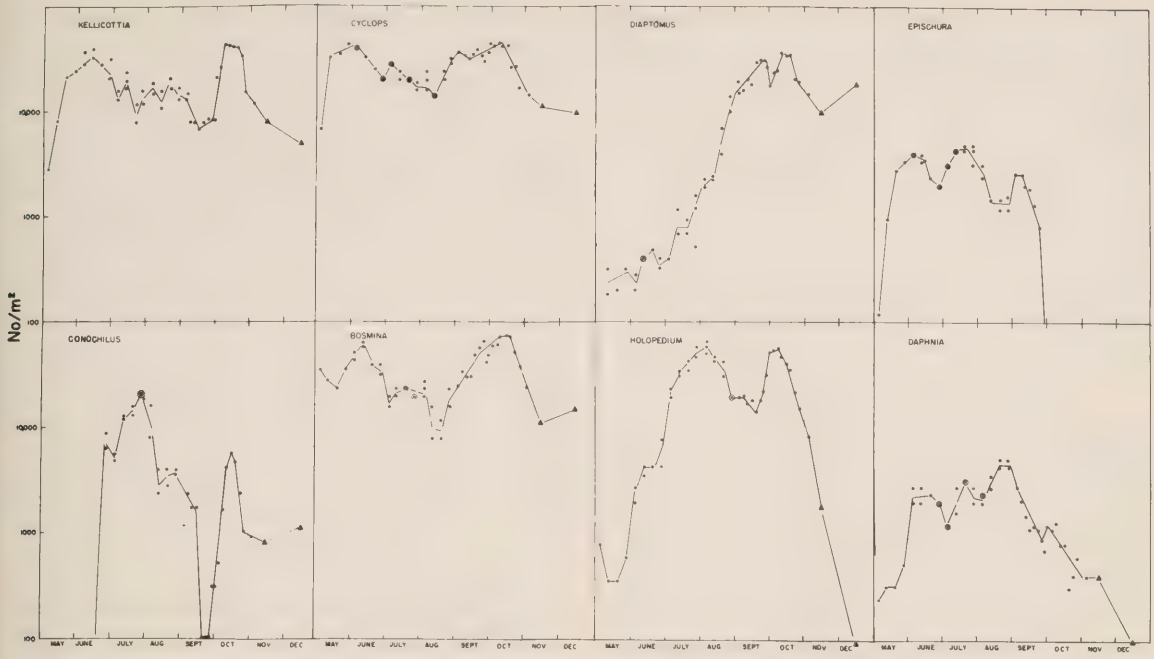


FIGURE 4.—Species counts (no./m² in 50-m vertical hauls at Stations 1 and 2. (Points represent a 4-day running mean, solid triangle indicates monthly mean, circle with dot indicates more than one sample with the same count. Note: the numbers of organisms are shown on a logarithmic scale.)

TABLE 4.—Copepod sex ratios.

Month	Species					
	Cyclops		*Diaptomus*		*Epischura*	
	F/M	F_2/F_1	F/M	F_2/F_1	F/M	F_2/F_1
Jan.-April	0.6		1.2		0.5	
May	0.6	2.8	1.5	0.7	0.7	1.3
June	2.6	1.1	1.1	1.9	0.7	1.4
July	1.9	1.0	1.5	1.1	1.0	1.1
Aug.	1.9	1.6	1.3	1.0	1.1	0.8
Sept.	0.8	2.2	1.2	0.9	1.4	0.9
Oct.-Dec.	1.0	2.0	1.3	0.9	1.0	0.5

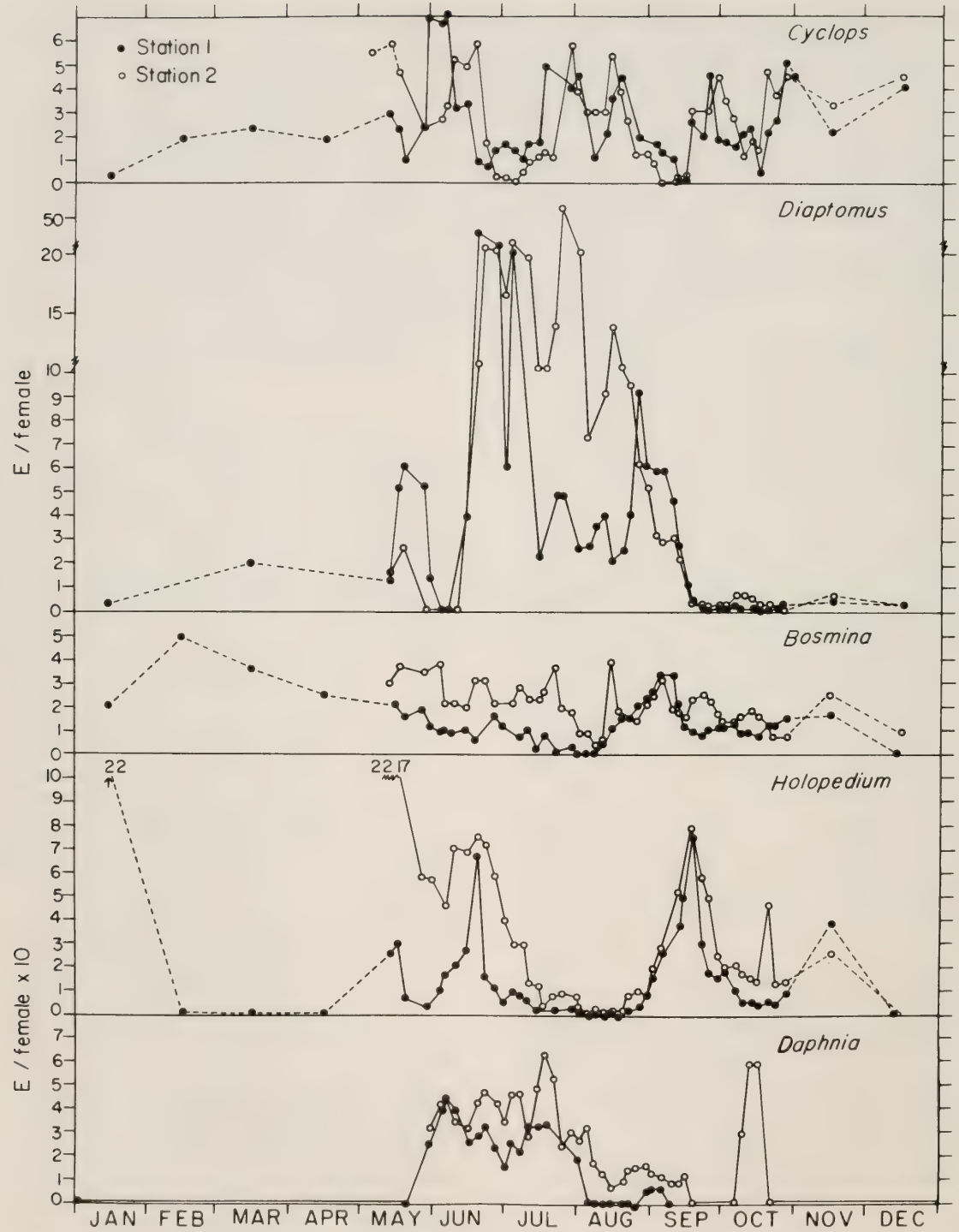
F/M Number of adult females/number adult males.
F_2/F_1 Number of adult females at Station 2/number of adult females at Station 1.

September 14. In contrast there was a tendency for *Diaptomus* females to be slightly more abundant than males throughout the year. The only period for which *Diaptomus* males were consistently more numerous than females was from June 22 to July 10. Included in Table 4 is the ratio of the number of female copepods at Station 2 to the corresponding number at Station 1. *Cyclops* was the only species in which the females were as numerous or more numerous at Station 2 than at Station 1.

EGG PRODUCTION

Counts were made of all readily identifiable eggs; these consisted of eggs in the brood pouch of cladocera and the egg sacks of *Cyclops* and *Diaptomus*. Rotifer species were not examined for eggs, while *Epischura* eggs were positively identified on only one occasion from a horizontal tow made at 1 m depth in August. It is possible that *Epischura* eggs develop close to the surface at depths of less than 1 m since they were not found at other standard depths sampled between 1 m and 65 m. Also other data, not presented here, indicate that the smaller size groups of *Epischura* were found closer to the surface than the adult stages.

The data presented in Figure 5 show the ratio of eggs per female for vertical samples collected at Station 1 and Station 2. It was noted in Table 4 that maximum numbers of copepod females occurred during the summer, June through September; *Cyclops* females were more numerous at Station 2 than Station 1 and *Diaptomus*


Station 1
Station 2
Cyclops
Diaptomus
Bosmina
Holopedium
Daphnia
22
22.17
E / female
E / female x 10
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC

females were in about equal numbers at both stations. In Figure 5 the eggs per *Cyclops* were about equally numerous at both stations. There were three and possibly four periods of maximum egg production for *Cyclops* females, i.e. June, mid-July through to the third week in August, and the last week of September through to the first week of November; the latter time interval could possibly be interpreted as consisting of two separate periods of egg production (late September and late October). *Diaptomus* females at Station 1 had two major periods of egg production, mid-June through mid-July and mid-August through the first week of September, with a period of relatively low egg production from mid-July to the end of August. At Station 2 there was no clear cessation of *Diaptomus* egg production from mid-June through to the first week of September. For a major part of this period there were more than 10 eggs per female being produced. There was also a brief period of *Diaptomus* egg production in mid-May.

The production of *Bosmina* eggs ranged between 0 and 0.5 per individual. From May through mid-August more eggs were produced at Station 2 than at Station 1 and thereafter the egg production was nearly equal at both stations. The summer minimum which occurred in the first 2 weeks of August was followed by a rise in the number of eggs in the first week of September continuing until the end of the third week of September. The summer maximum of adult *Bosmina* shown in Figure 4 occurred approximately 1 week after that of the eggs while the maximum standing stock of *Bosmina* (which occurred in mid-October) was preceded by the production of eggs 3 to 5 weeks earlier. *Holopedium* exhibited two clearly defined peaks in the production of eggs, from the first to the third week of June and again from the first to the third week of September. The corresponding maximum in the standing stock of *Holopedium* shown in Figure 4 occurred from the second week of July through to August 25 and from September 27 to about October 20; the summer minimum occurred between the two peaks. The production of *Daphnia* eggs took place from June to mid-September with a second brief rise in egg production during mid-October at Station 2. The numbers of eggs produced per female at Station 2 by all species of cladocera was generally greater or equal to that at Station 1. It should be noted that the latter was found for both the prefertilization period in May as well as during the period of nutrient additions.

FIGURE 5.—Ratio of the number of eggs to the number of adult females. The data from 50-m vertical samples at Stations 1 and 2 have been averaged to give a 4-day running mean ratio. Note: scale changes for different species.

ZOOPLANKTON BIOMASS

The wet weights for 1970 50-m vertical hauls at Stations 1 and 2 were combined and expressed as a monthly mean wet weight (g/m^2) together with the range about the mean weight (Figure 6). Included in Figure 6 (below) are individual weights for the 1969 sampling. The maximum wet weight in 1969 never exceeded 1 g/m^2 whereas in 1970 the weights ranged as high as 15 g/m^2. The average wet weight of zooplankton during the period May through October was approximately 0.5 g during 1969; for the same period in 1970 the average weight was 10 times larger, i.e. 5.3 g. The sample weights increased at a rate of 3% per day May through July to a maximum average wet weight of 8.6 g/m^2; there-

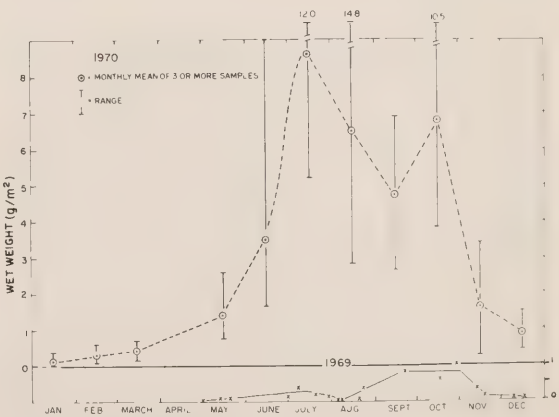


FIGURE 6.—Zooplankton wet weight (g/m^2) for 50-m vertical hauls. In the lower part of the figure, the points marked "x" indicate individual weights (g/m^2) for 1969 samples.

after the weights declined at an average rate of 1.5% per day to the December biomass of 0.9 g/m². The actual rate at which the mean weight of zooplankton declined in any one month following July was greater than the average computed above due to the increase in biomass in October. Inspection of Figures 3 and 4 indicates that the decline in biomass seen in August was a result of fewer numbers of *Epischura, Bosmina,* and *Holopedium. Epischura* never reached its earlier level of abundance after August and was virtually absent from the samples by October whereas most other species, *Daphnia* excepted, showed an increase in abundance in October which gave rise to the October increase in biomass.

Dry weights of Great Central Lake zooplankton (determined by the freeze-dry method) ranged from 14% to 26% of the wet weight with a mean of 19%. The variation in the percentage dry weight was directly attributable to the species composition of a sample. For example, the dry weight of *Holopedium* was 14% of their wet weight, whereas the dry weight of *Cyclops* was approximately 26% of the wet weight. The average dry weights of the summer zooplankton (May through October) integrated over a 25-m column, i.e. the depth range in which most zooplankton were concentrated, for 1969 and 1970 was 4 mg and 40 mg/m³ respectively (from Figures 2 and 6).

TABLE 5.—Length-weight measurements of adult crustaceans.

Species	Mean length *(Microns)*	Wet weight *(Micrograms)*
Cyclops	960	6
Diaptomus	1,100	11
Epischura	1,500	66
Bosmina	300	4
Holopedium	900	17
Daphnia	900	10

Length-wet weight determinations were made for different sizes and stages of the common crustacean species and the data are summarized in Table 5. The data in Table 6 were obtained by multiplying the maximum concentration (no./m³) of a species within particular depth intervals (Figure 2) by their respective weight from Table 5, thereby providing a measure of biomass with depth. Included in Table 6 are the mean July temperatures within the respective depth intervals. Nearly 60% of the total biomass occurs in the upper 10 m where the mean temperature was about 18°C. In the thermocline, from 10 to 20 m, with a temperature range from 12° to 6°C (mean temperature, 9°C) the biomass was about 50 mg/m³ or approximately 30% of the total. From 20 to 30 m depth the biomass was about 8% of the total. The remaining 3 to 4% of the total biomass occurred below 30 m (30 to 60 m). While these data were derived from July sampling it should be noted that the general distribution of the biomass with depth was similar throughout the period of thermal stratification, i.e. June to October.

DISCUSSION

The zooplankton standing stock in 1970 shows a phenomenal increase over 1969. This can be largely attributed to the affect of the nutrient additions upon the rate of primary production. The results of Parsons et al. (1972) demonstrate a marked increase in the rate of primary production within the upper 5 m; at the same time there was little or no change in the standing stock of primary producers. While experiments and observations of a direct relationship between particular species of primary and secondary producers have not been attempted, the obvious inference is that the zooplankton through increas-

TABLE 6.—Relative biomass of July crustacean zooplankton in various depth intervals (from Figure 2).

Depth range *(m)*	$m\bar{T}$ °C	Mean maximum biomass (mg/m³)						
		Cyclops	*Diaptomus*	*Epischura*	*Bosmina*	*Holopedium*	*Daphnia*	Total
0-10	18	--	1.3	39.6	7.2	51.0	.1	99.2
10-20	9	1.2	.3	19.8	2.8	28.9	.5	53.5
20-30	6	3.1	.3	4.9	1.2	3.4	1.8	14.7
>30	<5	.6	--	2.3	.7	1.7	.2	5.6

ing stock size were able to utilize the higher rates of primary production.

It is also apparent that the higher biomass in 1970 cannot be entirely attributed to fertilization since the biomass in May (prefertilization) was also higher than any of the 1969 values. However, the nearly continuous production of eggs by most species and the maintenance of an increased standing stock over a 6-month period are indicative of a direct relation between zooplankton and nutrients. It is also noteworthy that there was no change in species diversity.

The techniques employed for wet weight determinations in this study have produced weights which are apparently lighter than would be obtained by other investigators. Wet to dry ratios in the literature suggest that the dry weight is 5% to 10% of the wet weight. Schindler and Noven (1971) employed a ratio of 6%, although their reason for using this particular value is not given; the present results indicate that the dry weight is 19% of the wet weight. Consequently, the present weights could be increased approximately three times for comparison with other studies. Thus in the lakes which range from oligotrophic to eutrophic, listed by the above authors, Great Central Lake has, in terms of its mean summer zooplankton biomass, changed from oligotrophic to oligotrophic-mesotrophic, i.e. 12 mg in 1969 to 120 mg dry weight/m^3 in 1970. In lakes producing sockeye salmon the mean abundance of zooplankton ranges from values which are less than 5 mg dry weight/m^3 to greater than 1 g dry weight/m^3 (Johnson, 1965). The mean concentrations in Great Central Lake have increased from the very low end of the range to values which are commonly reported for some of the larger sockeye producing lakes, e.g., Babine Lake.

Johnson (1965) concluded that there was a general relationship between the rate of growth of underyearling sockeye and zooplankton abundance. However, he also suggested that with increasing fish density food abundance was supplanted by a space effect as a limiting factor. In Great Central Lake the underyearling sockeye in October of 1970 were ca. 30% heavier than fish caught in October of 1969 (Parsons et al., in press; Barraclough and Robinson, 1972). In addition to the increase in weight these authors report (on the basis of the number of adult salmon spawning) that the number of sockeye fry in the lake were from two to five times more numerous than in the previous year. Assuming an initial weight of 120 mg for individual fry of each year the respective rate of growth over their first 200 days of lake residence was 0.9% and 1.2% per day for 1969 and 1970 respectively. The increased growth rate of sockeye in 1970 is less than might be anticipated from the 10-fold increase in zooplankton abundance. Johnson's data (1965) indicated that a population density of 1 fish per m^2 might be the point at which space becomes a factor limiting growth. The maximum estimate of 1×10^7 sockeye in Great Central Lake during 1970 is approximately 1 fish in every 5 m^2. Consequently it appears unlikely that the density of the fish population in Great Central Lake limited their growth.

Among other factors which limit growth of sockeye, Foerster (1968, Figure 45) indicates that temperature has a major affect upon growth and the efficiency with which food is utilized. The optimum temperature for food conversion for sockeye lies between 10° and 15°C. At higher or lower temperatures the efficiency of food conversion decreases, especially at temperatures in excess of 20°C or less than 6°C. The laboratory studies of Brett et al. (1969) with fingerling sockeye support the findings reported above. In their experiments 15°C was found to be the optimum temperature for growth at high rations; however, maximum efficiencies with which a ration was utilized occurred at lower temperatures, e.g. the maximum food conversion efficiency of 40% with a 0.2% increase in fish weight per day occurred at a temperature range of 8° to 10°C and a ration of 1.5% of the fish weight/day. Temperatures between 5° and 17°C were found to provide the laboratory fish the optimum conditions for conversion efficiencies and growth. In Great Central Lake, during their first 200 days of lake residence, the underyearling sockeye concentrate at depths of 50 m or greater during daylight; with the approach of sunset the fish move to shallower depths and by nightfall the major portion of the population

is at depths between 10 and 20 m while some fraction of the population occur in the upper 10 m. This pattern of vertical migrations appears to be repeated daily (Barraclough and Robinson, 1972). Narver (1970) has reported similar vertical movements for sockeye populations in Babine Lake. For the greater part of the day the salmon in Great Central Lake are at temperatures of 4° to 5°C, a somewhat shorter period (ca. 6 hr) is spent at temperatures of 6° to 12°C (10 to 20 m depth) while a relatively brief period (ca. 1 hr) may be spent at temperatures ranging from 14° to 23°C (0-10 m depth). Details of the time actually spent at different depths by the sockeye are reported by Barraclough and Robinson (1972). It is apparent that the fish are utilizing the maximum concentrations of prey which occur at above optimum temperatures in the upper 10 m for very short intervals. Consequently in assessing the relationship between the increased abundance of prey brought about through fertilization and the sockeye it should be noted that possibly 60% of the total biomass, i.e. the portion in the upper 10 m, may be only partially available to the fish (Table 6). Furthermore, some prey species because of their size (rotifers) or structure (*Holopedium*) may not be a particularly useful food source for the salmon. *Holopedium*, for example, was among the largest and most numerous species of crustaceans in the lake; however, a large fraction of their biomass is comprised of a gelatinous material of dubious food value. The difference in the wet to dry weight ratio between *Holopedium* and other zooplankton (14% to ca. 26% respectively) attests to the water composition of *Holopedium*. The quality of prey together with the observations of Foerster (1968) and Brett et al. (1969) emphasize the need for caution in interpreting predator-prey relations. In the present instance, the benefits of the fertilization appear to have been only partially transferred to the sockeye salmon. Since the thermal structure of the lake is a factor beyond immediate control, it would be interesting to consider possible benefits from the addition or deletion of some prey species and to attempt to shift the level of primary and secondary production to depths and temperatures favoring sockeye salmon growth.

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THE FERTILIZATION OF GREAT CENTRAL LAKE
III. EFFECT ON JUVENILE SOCKEYE SALMON

W. E. Barraclough and D. Robinson[1]

ABSTRACT

Nutrient levels and rates of primary production in nursery lakes are factors which may limit production of sockeye salmon. This paper describes the effect of artificial fertilization on feeding behavior and growth of juvenile sockeye salmon in Great Central Lake, Vancouver Island, British Columbia. Underyearling sockeye salmon grew 30% larger in 1970 than in 1969 as a result of adding 100 tons of fertilizer to Great Central Lake. The growth pattern for the whole population was complex, however, and the increase in size of juvenile sockeye was not as much as had been expected from the increase in quantity of their food organisms. The fact that the sockeye did not appear to appreciably crop the high epilemnetic concentrations of zooplankton during July and August 1970 may have been partly due to avoidance of high temperatures by the fish.

Decomposing carcasses of anadromous fish, such as the sockeye salmon (*Oncorhynchus nerka*), contribute to the fertilization of nursery lakes following spawning in the lake. In most instances the extent of this fertilization is not known but the removal of maturing sockeye by a commercial fishery may deny lake waters of their essential nutrients and contribute to lowered productivity. Particular attention has been focussed on the imbalance of phosphate in the natural fertilization of lakes from decomposing salmon carcasses (Krokhin, 1959) and the suggestion has been made (Krokhin, 1967) that a positive balance should be maintained by the artificial replacement of the phosphate with inorganic fertilizers.

Early studies carried out in a small unstratified lake in Alaska (Nelson and Edmondson, 1955; Nelson, 1958) showed that the addition of phosphate and nitrate fertilizer resulted in increased length and weight of sockeye smolts leaving the lake. The potential role of a natural imbalance of phosphate in nursery lakes on sockeye salmon is emphasized in the following quotation from Foerster (1968):

> One wonders whether sufficient significance has been given to this feature of the phosphate balance. With sockeye populations in all areas showing such evident declines, despite legislation on regulation and limitation of fishing, it might well be that some basic factor such as this may be having a much more limiting effect on productivity than seems apparent. In addition to the smaller amounts of phosphorus introduced into a lake in the carcasses of fewer sockeye spawners, there may also be occurring a steady decline in the phosphate content of the runoff waters as the phosphates of the soil and rock become leached out over the years. Future studies of the phosphate balance of sockeye-producing waters and the direction of its trend may prove most enlightening. Addition of suitable fertilizers may be found advantageous.

In recent years it has become more evident that suitable fertilizers should not only include phosphates but also other nutrients, including trace elements, in order to increase aquatic productivity (Goldman, 1960, 1964).

The theory and application of adding natural fertilizers to aquatic environments has been practiced in fish farming for many centuries. Parsons et al. (in press; 1972) have presented data on various aspects of lake fertilization studies carried out by others. In summary of these findings, there is much evidence to show that the larger the sockeye smolts at the time of seaward migration, the higher the percentage return from the sea (Burgner, 1962; Ricker, 1962). Since food supply is one of the important factors

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governing growth, the effect of increasing the food supply to underyearling sockeye salmon through artificial fertilization of Great Central Lake, B.C., is presented here. It has already been established (Parsons et al., in press; 1972) that the waters of Great Central Lake are relatively unproductive of sockeye salmon, the average size of yearling smolts at the time of seaward migration being much smaller than in Babine Lake, B.C. (63 mm versus 79 mm) (McDonald, 1969). The average size of yearling smolts from 14 other lakes in Washington, British Columbia, Alaska, and Kamchatka is larger than the yearling smolts from Great Central Lake (Foerster, 1968). In the following account particular attention is given to changes in size of juvenile sockeye salmon in Great Central Lake associated with changes in their food supply prior to and after the addition of inorganic nutrients (see Parsons et al., 1972; LeBrasseur and Kennedy, 1972).

STUDY AREA

Great Central Lake (Figure 1) is located in central Vancouver Island, British Columbia. The lake is about 33 km long and varies between 1 and 2.5 km in width. The shoreline length is 72 km and the surface area is ca. 51 km^2. Elevation of the lake surface is 83 m above sea level and the mean depth is 200 m, with a maximum depth of about 280 m. The outlet of the lake runs into the Stamp River. Most of the shoreline slopes very abruptly into deep water. This feature is an important factor in regulating horizontal distribution of juvenile salmon in the lake, by providing a maximum amount of the lake surface available to juvenile sockeye.

LAKE SPAWNING

A brief account of the spawning sites of the sockeye salmon is presented here because the location of the in-lake spawning grounds is an important factor in the emergence of the alevin and dispersal of the fry at the time of their initial intake of food. Little or no published information is available on the migration and spawning of adults in the lake. Mr. F. C. Boyd of the Department of the Environment has kindly granted permission to refer to his internal manuscript reports on the subject.

Adult sockeye salmon bound for Great Central Lake first enter the Stamp River as early as the first week in June. This migration up the Stamp River continues through June, peaks in July, and in most years, ends in early August. The peak

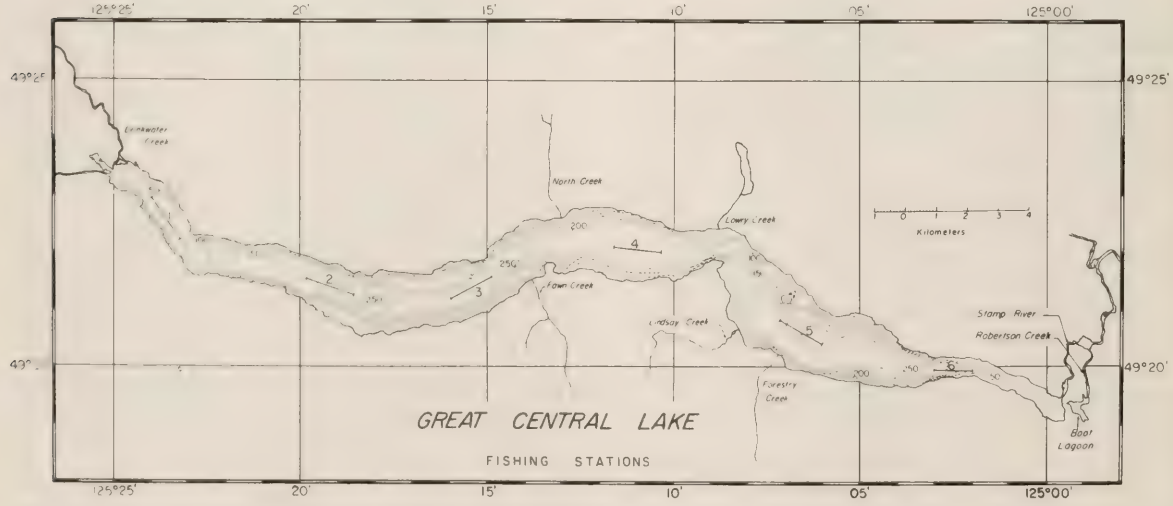

FIGURE 1.—Great Central Lake showing the six fishing stations and depth contours in meters.

of migration may not occur until the first week in September. It takes between 2 and 5 days for the sockeye to migrate up the Stamp River into Great Central Lake, depending on the water levels in the river. The fish remain in the lake but do not commence to spawn until the latter part of September. Great Central Lake is one of the few lakes in British Columbia where most of the spawning occurs in areas along the lakeshore rather than in tributary streams. Only a few hundred sockeye spawn in tributary streams a short distance away from the lake. Drinkwater, Lindsay, and Fawn Creeks (Figure 1) receive most of the stream spawners.

Lakeshore spawning commences in the last week of September, reaches a series of peaks in three principal locations during October, and ends in November. About 50% of the spawning occurs along 4.63 km of lakeshore between Lindsay Creek and Forestry Creek, 30% along 1.1 km of shoreline west of Fawn Point, and 20% along 1.6 to 4.8 km of lakeshore off North Creek. Redds were found at depths between 0.6 and 24 m but most were between 12 to 15 m. Spawnings were observed by scuba divers at depths as great as 41 m. It is now realized that the location of separate major in-lake spawning areas is important in providing the potential basis for the immediate and rapid distribution of juvenile sockeye throughout the lake, shortly after the fry emerge from the gravel and commence to feed. Two spawning areas are adjacent to the lake area where fertilizer was applied (see Parsons et al., 1972).

METHODS

LOCATION AND DISTRIBUTION OF JUVENILE SOCKEYE SALMON

A high frequency (200 kHz) moist paper recording echo sounder (Furuno model No. FNV-3000)[2] was used to locate the young sockeye in the lake and monitor their horizontal and vertical distribution. During the day, young sockeye are generally distributed throughout the lake at depths between 45 and 90 m, but are most abundant at about 65 m. They commence to migrate toward the surface about half an hour before sunset. In the summer months at civil twilight, when the sun is 96° from the zenith (or 6° below the horizon) they are distributed irregularly in density between 5 and 30 m. At nautical twilight when the sun is 102° from the zenith (or 12° below the horizon) the juvenile sockeye form a layer between the depths of 10 and 20 m, with a maximum density of about 14 m. At night during the winter months they are distributed more uniformly between 20 and 60 m. In summer the downward migration commences shortly before sunrise and is usually complete 15 to 30 min after sunrise.

The young sockeye were sampled with midwater trawls. Sampling commenced at night when the fish were in a layer between 10 and 20 m. Samples were also collected during daylight at different depths throughout the depth range of the young sockeye. The depth of trawling was adjusted to coincide with the depth of maximum fish concentration as shown by the echo sounder traces.

FISHING GEAR

A trawl net with a mouth opening 3 m wide, 6.1 m deep, and 17.7 m long was towed at 2.7 to 3.2 km/hr by a single vessel, the *Decibar*, to sample the sockeye between the depths 5 and 25 m. Three mesh sizes of knotless nylon netting were used in the construction of the net: 5 cm and 2.5 cm stretched mesh in the body and 1.3 cm in the cod end. The cod end measured 1.2 m wide by 1.8 m deep at the mouth and it tapered to a blunt end about 76 cm in diameter. A standard Henson plankton net (350μ mesh) 76 cm in diameter at the mouth, was secured to the blunt aft end of the cod end to retain the smallest juvenile sockeye and minimize the loss

[2] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

of their minute scales by abrasion against netting in the main cod end of the trawl.

An Isaacs-Kidd midwater trawl was towed from the *Decibar* to sample the juvenile sockeye at depths greater than 25 m and to evaluate the fishing capabilities of the large midwater trawl towed at the same depths. The mouth opening of this trawl was 1.9 m^2 and the net was constructed of 6.3 mm stretched mesh knotless netting.

FISHING STATIONS

Juvenile sockeye were sampled with trawls taken at intervals of about 3 weeks at 6 different stations (Figure 1). Most of the tows were of 30 min duration but some tows were shorter, when the echo sounder traces indicated that young sockeye were especially abundant between 12 and 14 m at night.

ANALYSES OF SAMPLES

The length of all fish was measured to the nearest millimeter from the snout to the end of the central rays of the caudal fin. This measurement is referred to as the fork length. Lengths of smaller fish were measured in a graduate tray under a binocular microscope; calipers were used for larger individuals.

All fish were weighed by fork length groups using a center-loading milligram balance (KERN Model No. T1226-1). Weights recorded are from "blot-dried" specimens. Moisture was blotted from the exterior of the fish, and gentle pressure was applied to the buccal cavity and branchial chamber to remove moisture from these spaces. Age was determined from scales using $\times 254$ projections of thermoplastic impressions.

Stomach analyses for food were done on fish selected to represent proportionally as complete a size range as possible. The food weight was measured by subtracting weight of stomach shell from weight of stomach plus food. The number of all species of food organisms were counted according to size and state of condition of each stomach examined.

RESULTS

FOOD OF UNDERYEARLING (AGE 0) SOCKEYE

During the latter part of March and up to mid-April, 1970, pre-mature fry[3] (24 to 28 mm fork length) with a small portion of the yolk sac remaining were caught at night at a depth of 14 m in midlake positions off the 3 major spawning areas. A few fry (28-30 mm) with empty stomachs were caught during the day at depths between 35 and 100 m in late March, and the first actively feeding fry (28 to 33 mm) were caught at depths between 12 and 55 m at night during the latter part of April. The number of fry caught at midwater depths increased in May at Stations 3, 4, 5, and 6 and reached a maximum in June at all stations. Fry continued to be caught in July and were still being caught in trawl nets at night in late August and early September. The fry and larger underyearling sockeye ate the same food organisms throughout the year, but the larger juvenile fish had more food in their stomachs.

Figure 2 shows the number and weight of all species of food organisms per underyearling sockeye (Age 0) from August, 1969, when inlake sampling began to April, 1970, when about 85% of the fish migrating were yearling smolts.[4] The percentage of the total number of the six major food categories from all the fish sampled for stomach contents through the same period is shown in Figure 3. A list of the different genera of food organisms found in the stomachs of juvenile sockeye from 1969 to 1971 is given in Table 1; the smallest is listed at the top of the column and the largest at the bottom.

Epischura was the predominant form (60%) in the stomachs in August, 1969 but was almost replaced by *Holopedium* (60-80%) from September to December (Figure 3). The incidence of

[3] "Embryo" is defined as a larva minus its yolk-sac. An "alevin" is a larva of an age following hatching but prior to yolk absorption. Following this stage the fish becomes a "fry" (cf. Bams, 1969).

[4] In 1969 ca. 86% of migrant smolts were yearling, 10% were 2 year old, and 4% were 3 year old. In 1970 ca. 85% of smolts were yearling and 15% were 2 year old.

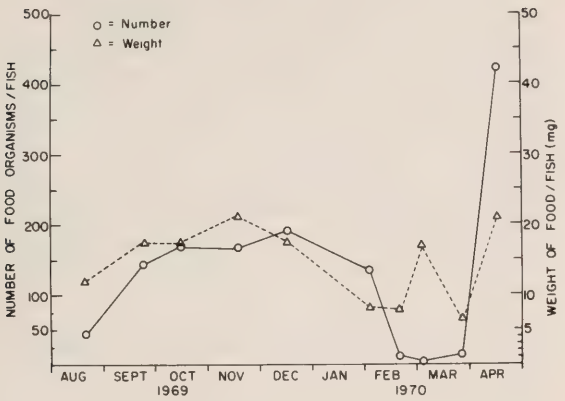

FIGURE 2.—Average number and weight of all food organisms (all species combined) per fish for underyearling sockeye salmon in Great Central Lake from August, 1969 to April, 1970.

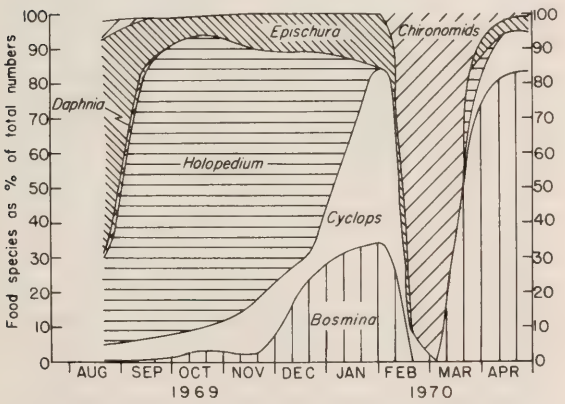

FIGURE 3.—Food of underyearling sockeye salmon expressed as a percentage of the total number of organisms from August, 1969 to April, 1970.

TABLE 1.—List of organisms found in juvenile sockeye stomachs.

Size range	Organism
mm	
0.3-0.6	*Bosmina*, usually *B. coregoni*
0.6-1.1	*Cyclops*, usually *C. biscuspidatus thomasi* and *C. vernalis*
0.9-1.2	*Holopedium gibberum*
0.9-1.5	*Daphnia*, usually *D. longiremis*
0.8-1.3	*Diaptomus*, usually *D. oregonensis*
2.0-2.5	*D. kenai*
1.1-1.9	*Epischura nevadensis*
3	Insects of the order Diptera (other than Chironomidae)
3-5	Insects of the family Chironomidae—larvae
8-11	Insects of the family Chironomidae—larvae
6-11	Larvae of the sculpin, *Cottus asper*

Bosmina and *Cyclops* increased gradually from less than 5% in August to a peak of 30 to 50% in January-February, 1970. Chironomid larvae were the only organisms eaten from February to early March and in turn were replaced by *Bosmina* (80%) in late March and April. The percentages of *Epischura* and *Holopedium* in the stomachs by number (Figure 3) and by weight (Figure 4) were similar from August to December. There was a pronounced difference between the percentages by number and by weight of *Cyclops* and *Bosmina* per fish. Although the percentage by numbers of both organisms per fish increased markedly between December, 1969 and February, 1970, the percentage weight per fish remained less than 7% for *Bosmina* and never exceeded 20% for *Cyclops*. The importance of the chironomid larvae in the diet of underyearling sockeye from February through March to early April, 1970 is more indicative when expressed as a percentage by weight (Figure 4) than by number of organisms (Figure 3).

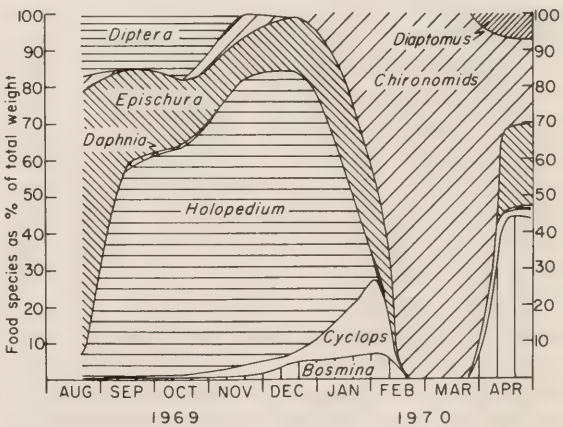

FIGURE 4.—Food of underyearling sockeye salmon expressed as a percentage of the total weight of organisms from August, 1969 to April, 1970.

The fry which emerged in late March and April, 1970 commenced to feed actively by mid-April and, as juvenile sockeye, they continued to increase their intake in number and weight of all food organisms throughout the summer,

reaching a peak in September-October (Figure 5). In August, 1970, 3 months after lake fertilization began, the underyearling sockeye had twice the number of organisms per stomach as in August, 1969 and contained about 60% more food by weight. The high consumption in September-October, 1970 represents an increase of about 45% in number of organisms, and 40% by weight, compared to the stomach contents per fish in the same period in 1969. A slight decline in number and a significant decline in weight of food organisms per fish was shown from November, 1970 to February, 1971; an abrupt increase occurred to a second high in March, which represented an increase manyfold over March, 1970. This increased food consumption occurred 1 to 2 months prior to their emigration from the lake as yearling smolts.

Five species of food organisms contributed chiefly to the diet of underyearling sockeye in Great Central Lake in 1970. In April and May *Bosmina* contributed about 50% of both the total number (Figure 6) and total weight (Figure 7) of all organisms found in their stomachs. The numbers of *Bosmina* consumed were insignificant throughout the rest of 1970 and the first 3 months of 1971. *Epischura* was the most important food organism from May to July (Figures 6 and 7) and was probably the principal source of energy for the rapid growth of the underyearlings during this period (see Figures 11 and 12). There was a transition in late July and August when *Cyclops*, *Holopedium*, and *Daphnia* gradually became more abundant in the stomach samples. In the 3 months which followed, September to November, *Cyclops* and *Holopedium* were the predominant genera. *Cyclops* continued in importance and formed about 50% of the number of food organisms to the end of January, 1971. However, during this period of 6 months *Cyclops* formed only 15 to 30% of the food by weight whereas *Holopedium* constituted 30 to 80% by weight. *Diaptomus* was first observed in the stomachs in the latter part of October, increased markedly in December and January, and was the predominant food organism by number in February and March, 1971. Thus *Diaptomus* was the most numerous food organism in the stomach samples just before

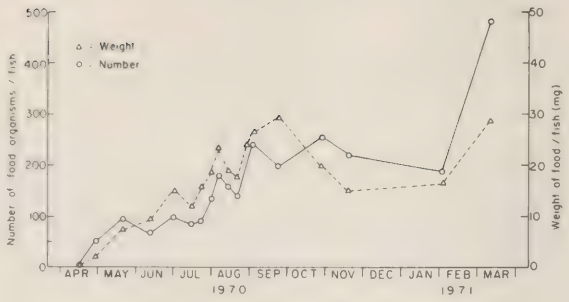

FIGURE 5.—Number and weight of all food organisms per fish, for underyearling sockeye salmon from April, 1970 to March, 1971.

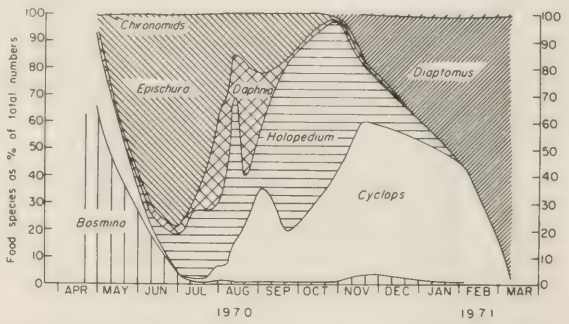

FIGURE 6.—Food of underyearling sockeye salmon expressed as a percentage of the total number of organisms from April, 1970 to March, 1971.

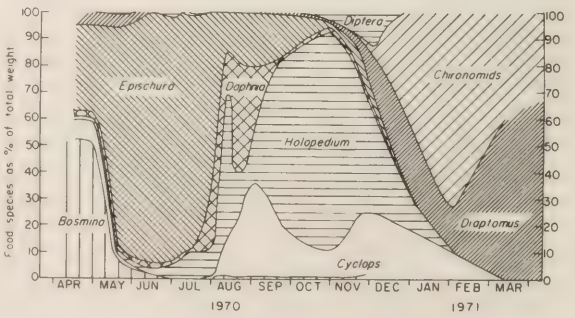

FIGURE 7.—Food of underyearling sockeye salmon expressed as a percentage of the total weight, from April, 1969 to March, 1971.

smolt migration in 1971. *Bosmina* was the most numerous in the previous year. The few chironomid larvae (Figure 6) in the diet of juvenile sockeye from December, 1970 to March, 1971, formed 30 to 70% by weight of all the food organisms (Figure 7). The importance of chironomid larvae during the winter months was observed also in the previous winter (Figures 3 and 4).

FOOD OF YEARLING (AGE 1) SOCKEYE

Those underyearling sockeye in Great Central Lake in 1969 which did not migrate to sea as yearling smolts in 1970, but remained in the lake for a second year, attained a mean length of only 51 mm and weight of 1.1 g between the latter part of April and May, 1970, whereas the migrating smolts had a mean length of 70 mm and weighed 3.5 g. The yearling sockeye which remained in the lake were collected from samples taken at all six stations and not from the end of the lake where smolts were schooling and heading seaward. Reference will be made later to the fact that the smallest size smolt, caught in the Robertson Creek weir (Figure 1) or in the nets set to capture smolts in the Stamp River, measured 55 mm and weighed 1.5 g.

Food organisms found in the stomachs of the yearling sockeye were similar to those eaten by the underyearlings during most of the year in 1970, but the yearling sockeye were more selective in cropping the larger forms of zooplankton (Figure 9). Both the underyearling and yearling sockeye fed heavily upon *Epischura* from May to July (Figures 6 and 9), but it was evident from the large numbers and weight of food organisms per fish (Figure 8) that the yearling sockeye elected to feed or were able to prey more heavily upon *Epischura* (Figure 9) than the underyearlings during September and October. Few yearling sockeye were caught in the trawls during the winter months of 1970-1971 prior to their migration as 2-year-old smolts. *Diaptomus*, *Holopedium*, and *Cyclops* were in the stomachs of these fish.

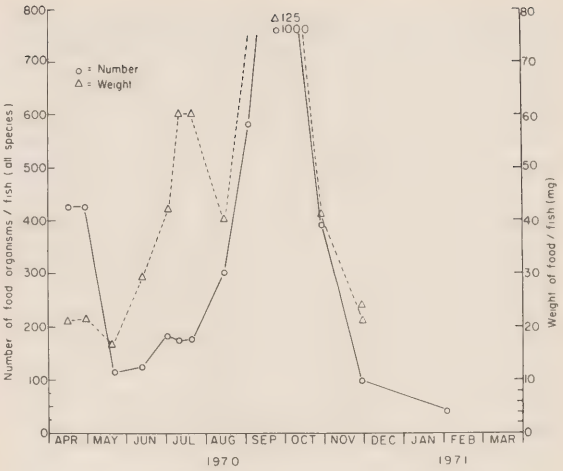

FIGURE 8.—Number and weight of food organisms of yearling sockeye salmon from April, 1970 to February, 1971.

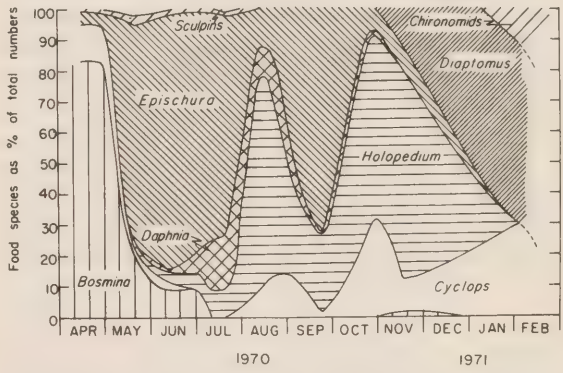

FIGURE 9.—Food of yearling sockeye salmon expressed as a percentage of the total number of organisms from April, 1970 to February, 1971.

DIEL FEEDING OF JUVENILE SOCKEYE

From midafternoon on June 17 to midday on June 18 a series of 11 tows, each of 15 min duration, were made with an Isaacs-Kidd midwater trawl. The trawl was towed through the middle of the densest portion of the stock during their

diel migration. The tows were made to determine what portion of different food organisms contributed to the salmon's ration during the day and night, as well as during the period of their diel migration. Data on depth and time of each tow, the number, size range, and mean length of sockeye caught, together with those sampled for the number and species of food organisms, and the weight of the food as a percentage of the body weight are given in Table 2.

The degree of freshness of food organisms was arbitrarily determined as fresh, fragmented, or largely unidentifiable. Fresh food was designated when no indication of digestion had occurred. The percentage of fresh zooplankton in the stomachs is given in Table 2. Depth of the densest portion of the layer of juvenile sockeye at different times of the day and night is indicated in Figure 10a by a broken line. The depth and time of each trawl tow relative to the depth of the fish is also indicated in Figure 10a.

The 24-hr data collection shows that in the day the densest portion of the layer of juvenile sockeye was formed at 75 m where the temperature of the water was 4° C; of the fish examined for stomach contents (Table 2) from tow No. 1, few food organisms per fish (Figure 10b) were noted and only 5% of the species were in fresh condition (*Bosmina*). The remaining species, *Epischura*, *Cyclops*, and *Daphnia*, were digested. Tow No. 2, through a less dense secondary layer at 105 m, indicated the same feeding pattern. Young sockeye commenced to migrate upward from 75 m between 1700 and 1800 hr. No differentiation in migration between underyearling or yearling sockeye could be detected at any level in the layer, either by net sampling or from high frequency echograms.

A tow just after sunset at a depth of 35 m revealed that the fish were eating *Bosmina* and *Cyclops* (Figure 10c) as they moved upward and 22% of the contents were in fresh condition. At 2200 hr the sockeye had passed 25 m where the heaviest concentration of *Cyclops* and *Daphnia* was located (LeBrasseur and Kennedy, 1972); in passing they had eaten *Cyclops* (Figure10c). It should be recognized, however, that there is a natural time lag between feeding at any depth and the time the fish was captured by the trawl at a shallower depth, as they migrated toward the surface.

At nautical twilight, most of the fish had completed their upward migration and were distributed in a layer between 10 and 20 m where temperatures ranged from 6° to 12°C (Figure 10a). Echograms indicated many of the juvenile sockeye salmon appeared to spend brief periods between 0 and 10 m at temperatures ranging from 14° to 23° C, during which time the young fish fed heavily upon *Epischura* (Figure 10c). In the 4 hr between the beginning and end of nautical twilight no feeding occurred (Table 2).

TABLE 2.—Diel feeding of juvenile sockeye; tows made with an Isaacs-Kidd midwater trawl, each of 15 min duration, over a 24-hr period from June 17 to 18, 1970 at Station 4 in Great Central Lake.

Tow No.	Depth of tow	Time (PST) at start of 15 min	Number fish caught	Size range underyearling	Mean length	Mean weight	Size range sampled for food	Mean length	No. sample for food	Total no. food organisms	No. of organisms per fish	% fresh	Weight of food as % body weight
	(m)			*mm*	*mm*	*mg*	*mm*	*mm*					
1	75	1449	47	23-40	32	292	28-40	33	10	190	19	5.5	1.1
2	105	1538	17	27-36	30	212	27-36	31	9	112	12	--	1.0
3	55	1820	21	27-38	32	272	27-38	33	10(1)[1]	67	7	--	1.0
4	35	2018	11	27-36	31	263	27-36	32	10	164	16	22	1.0
5	18	2142	6	26-36	31	282	26-36	31	6(2)	132	22	46	1.6
6	14	0023	71	26-41	32	315	26-41	33	11	537	49	6	1.7
7	19	0254	50	26-39	32	296	28-39	34	10(1)	257	26	--	1.5
8	62	0517	14	28-39	32	271	28-39	32	14(4)	586	41	64	2.1
9	68	0738	10	29-37	33	320	29-37	33	9	447	50	84	1.6
10	70	0945	9	29-39	33	278	29-39	33	9	543	60	34	1.6
11	75	1159	6	31-39	35	353	31-39	35	6	324	54	2	2.1
				Time of sunset		2011	Time of sunrise			0350			
				Time of nautical twilight		2201	Time of nautical sunrise			0200			

[1] Number in parentheses is number of items in sample which contained no food in stomachs.

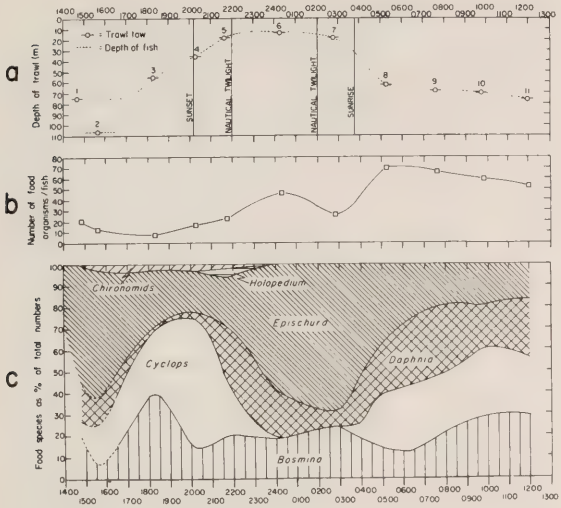

FIGURE 10.—(a) Depth of the densest portion of the layer of juvenile sockeye salmon at different times of the day and night from June 17 to June 18, 1970 is indicated by a broken line. A secondary layer is shown at 105 m for a 2-hr period. The depth of each tow with a midwater trawl is shown relative to the depth of the fish. (b) Number of all food organisms of underyearling sockeye. (c) Food species of underyearling sockeye salmon expressed as a percentage of the total number of organisms.

A second feeding period was noted at the time of the diel migration downward. Stomach samples from juvenile sockeye collected during this period contained many fresh *Daphnia* and *Cyclops* in tows 8 to 10. Only 2% of the zooplankton in the stomachs of sockeye caught at midday were in a fresh condition (Table 2), which indicates a marked reduction in feeding activity.

GROWTH OF UNDERYEARLING SOCKEYE

The average size of underyearling sockeye (Age 0) in 1969 and 1970 in Great Central Lake is shown in Figures 11 and 12. A total of 1,760 underyearling sockeye were caught in 1969 and 20,783 fish in 1970 from all six stations. A complete record of all data on which this analysis is based has been reported by Barraclough and

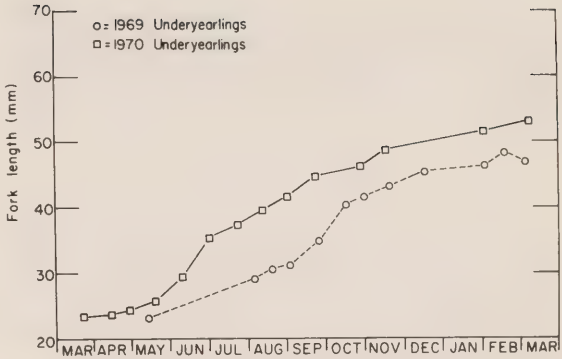

FIGURE 11.—Average length of underyearling sockeye salmon in each month, 1969 and 1970.

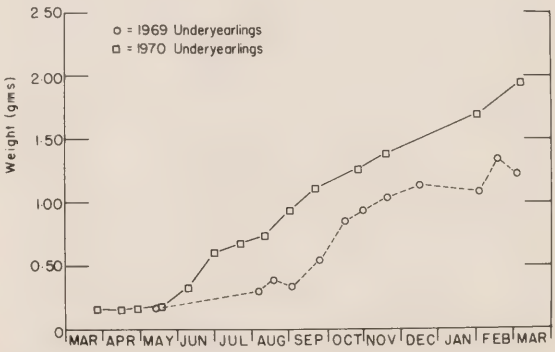

FIGURE 12.—Average weight of underyearling sockeye salmon in each month, 1969 and 1970.

Robinson (1971).[5] Although little data on the size of in-lake juveniles prior to August, 1969 are available, it is evident that a marked initial increase in length and weight of underyearlings occurred from June to July, 1970 at a time when sustained additions of nutrients were made to the lake. Growth continued steadily during the rest of 1970 and through winter months in 1970-1971.

[5] Barraclough, W. E., and D. G. Robinson. 1971. Length, weight, age and food of juvenile sockeye salmon (*Oncorhynchus nerka*) from Great Central Lake, British Columbia, May 1969 to February 1971. Fish. Res. Board Can., Manuscr. Rep. No. 1128, 268 p.

In October, 1970, when fertilization was discontinued, the underyearling sockeye salmon were about 30% heavier than the fish caught in October of 1969.

DISCUSSION

The period of freshwater growth is a very important stage in the natural production of juvenile sockeye. It is one in which mortality may be high, particularly in the very early stages of their growth. An abundant food of the optimum size readily available for the fry to prey upon is one factor which increases their survival rate (LeBrasseur et al., 1969). LeBrasseur and Kennedy (1972) determined that the biomass of zooplankton in May, 1970 before fertilization was greater than at the same time in 1969. At this time the numbers of fry caught in the midwater trawls began to increase and the catches were greatest, reaching a maximum in June at all stations shortly after fertilization commenced. LeBrasseur and Kennedy (1972) have demonstrated that the phenomenal increase in standing stocks of zooplankton in 1970 over 1969 was attributable to the sustained additions of nutrients. It is evident that the young sockeye fed very heavily (Figures 6 and 7) upon the increased number of *Epischura* in the lake (LeBrasseur and Kennedy, 1972). *Epischura* reached their greatest abundance in the upper 10 m in June when the average surface temperatures was about 15°C which was ca. 5° lower than that in July. In their diel migration, the young sockeye are able to take advantage of the most favorable temperature for food conversion for sockeye, which lies between 5° and 17°C, with a general physiological optimum at 15°C (Foerster, 1968; Brett et al., 1969). This may account for the rapid rate of growth in June compared with July.

Although the increase in length was greater in any one month in 1970 than it was in the same month in 1969, the increase in weight of about 30% in October, 1970 was less than expected from the 10-fold increase in zooplankton abundance reported by LeBrasseur and Kennedy (1972). The underyearling sockeye in the lake in 1970 were the progeny of a large escapement of 72,000 adults in 1969 and a large number of new recruits could be expected. Since most of the spawning occurred along the lakeshore it was not possible to determine the number of fry that entered the lake, particularly when it was discovered that fry were always caught in the trawls from March to August. An estimate of the total numbers of sockeye in the lake was calculated from the fish targets recorded on the high-frequency echo sounder during surveys of of the lake conducted once every 3 weeks throughout the year. From this analysis, coupled with pertinent catch data from each tow, a maximum estimate of 1×10^7 juvenile sockeye was determined. Johnson (1961) suggests that above a threshold concentration of 5,000 fish per hectare crowding may affect growth. LeBrasseur and Kennedy (1972) have demonstrated that the lake is sufficiently large that density of even a maximum estimate of 1×10^7 juvenile fish could not have been a limiting factor in their growth. However, the movement over a distance of 8 km in 1 day of large layered masses of juvenile fish in August (observed with high-frequency echo sounder) from one locality where the food source became depleted (O.D. Kennedy, personal communication) to another where food was abundant suggests that fish density may have been a seasonal factor.

The size of the yearling smolts leaving the lake from April to June each year was always larger than the same year class of juveniles caught at the six regular trawling stations during the same period because the migrating smolts school near the outlet of the lake. In 1969 the 781 yearling smolts caught in the Robertson Creek weir averaged 67.5 mm in length and 2.6 g in weight. In 1970 the average length of 1,423 yearling smolts was 71 mm and 3.5 g. In 1970 the average length of the yearling smolts decreased from 72 mm in April and May to 68 mm in June. The largest yearling smolts migrated first in April and May together with the 2- and 3-year-old smolts, and in June, almost all the smolts were smaller yearlings.

In April, 1971, 589 yearling smolts were sampled from the weir at Robertson Creek. Their average length and weight was 79 mm and 4.8 g. During this period the largest yearling smolts

ever recorded from the weir were taken, ranging from 90 to 95 mm. In May, 1971 the average length of 1,582 yearling smolts was 71 mm and a weight of 3.7 g. This average length and weight was the same as that of all yearling smolts sampled in 1970. In June, 1971, 3,012 yearlings were sampled and the smolts averaged 66 mm in length and 3.3 g in weight. It has been noted already that the smallest yearling smolt ever caught at Robertson Creek weir was 55 mm.

In conclusion, from the data presented here it is apparent that the total lake population of young sockeye salmon took advantage of the extra zooplankton ration (mainly *Epischura*) and that the average weight of individual fish of the in-lake population was 30% larger than in the previous year. However, the mechanism whereby this overall average increase in growth was observed is complex. The explanation offered is that the first fry to enter the epilimnion of the lake in April and May could take the greatest advantage of the increased zooplankton standing stock in June, when the average surface temperature was ca. 15°C. The following year (1971) this resulted in the migration of a group of 1-year-old smolts which were the largest (90-95 mm) ever observed from the lake. Fry which entered the lake in June and July could not take the same advantage of the zooplankton standing stock because the surface temperature was >16°C, and this reduced their feeding efficiency (Foerster, 1968). Thus increases in temperature of the epilimnion through the long period of fry emergence decreased the apparent benefit to late-hatching fish. However, in spite of this, most of the fry hatching later in the year achieved a length greater than 55 mm and migrated from the lake in June 1971; under normal conditions it is believed that these fry would not have reached 55 mm and would have migrated the following year as 2-year-olds. Preliminary examination of the scales from juvenile sockeye in 1971 reveals an absence of a winter check on many scales which suggests that the high concentrations of zooplankton persisting through the winter enabled many fish to smoltify and leave the lake. The combination of an early run of very large 1-year-old smolts, combined with this later run of much smaller smolts, tended to reduce the overall apparent effectiveness of lake fertilization. Thus the real effects of fertilization seem likely to be greater than would be judged from considering only changes in overall mean size of smolts.

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ESCAPE BEHAVIOR OF THE HAWAIIAN SPINNER PORPOISE (*Stenella* cf. *S. longirostris*)

WILLIAM F. PERRIN AND JOHN R. HUNTER[1]

ABSTRACT

Incidental mortality of porpoise (Cetacea, Delphinidae) occurs in the tropical tuna seine fishery. Experiments were carried out in a crowding chamber to determine behavioral responses of trained and naive Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*) to barriers of purse-seine netting, monofilament webbing, polyvinyl sheeting, rows of floats, and openings of various dimensions in a net wall. The object of the experiments was to generate information to be used in development of rescue gear and methods for the fishery. Openings of less than 1.5 m in width and/or 1 m in depth markedly inhibited escape. Negative effect of a line of floats across an opening at the surface was pronounced. Barriers of visually and acoustically relatively transparent monofilament webbing and polyvinyl sheeting were not apparently detected by porpoise prior to physical contact. Recommendations pertaining to potential design of rescue gear are presented.

Incidental mortality of porpoise occurs in the American purse-seine fishery for tropical tunas (Perrin, 1970). In 1970, the National Marine Fisheries Service began a program of research to develop improved gear and methods to reduce the porpoise mortality due to tuna seining. This paper reports the results of experiments on the responses to netting and other barriers by the Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*), a form closely related to one of the species involved in the tuna fishery.[2] We studied the response of the spinner porpoise to barriers of net, transparent monofilament nylon webbing, transparent polyvinyl sheeting, rows of floats, and to openings of different dimensions in a net wall. The results of these studies will be applied in the design of an escape opening in the tuna purse seine. The experiments were carried out at Oceanic Institute, Oahu, Hawaii, in May, June, and July 1970.

METHODS AND MATERIALS

THE ANIMALS

Three of the five porpoise (Table 1) used in the experiments had been in captivity at Oceanic Institute and Sea Life Park for various lengths of time and are referred to below as the "trained porpoise"; the remaining two, referred to below

TABLE 1.—Hawaiian spinner porpoise (*Stenella* cf. *S. longirostris*) used in behavioral experiments.

Name	Date of capture	Sex	Weight at time of capture
			kg
Trained porpoise			
Waimea	Mar. 6, 1969	Male	50.0
Nani	Dec. 4, 1969	Female	59.2
Nohea	Dec. 4, 1969	Male	65.9
Naive porpoise			
Westward	June 11, 1970	Female	72.7
Moana	July 9, 1970	Female	51.3

[1] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

[2] Taxonomic note: The spinner porpoise of Hawaii has been variously referred to *Stenella longirostris* Gray 1828, by Nishiwaki (1967) and Tomich (1970), and to *S. roseiventris* Wagner 1846, by Fraser (in Morris and Mowbray, 1966) and Rice and Scheffer (1968). The spinner porpoise of the tuna grounds of the far eastern Pacific has been referred to *S. microps* Gray 1846 (Miller and Kellogg, 1955; Handley, in Hester, Hunter, and Whitney, 1963; Nishiwaki, 1967; Pilson and Waller, 1970) and to *S. longirostris* (Rice and Scheffer, 1968; Harrison, Boice, and Brownell, 1969). No critical review of the genus has been accomplished since True's work on the Delphinidae in 1889. The usage here of *S. longirostris* for the Hawaiian spinner is provisional pending the results of taxonomic studies underway at the Southwest Fisheries Center and elsewhere.

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as the "naive porpoise," were freshly captured, were not exposed to any training procedures prior to the experiments, and were tested immediately upon arrival at the Institute.

THE APPARATUS

The crowding chamber (Figure 1) was constructed in a large pool at the Oceanic Institute. The pool, known as "Bateson's Bay," is roughly circular, 24.7 m across at its greatest diameter, and approximately 4 m deep at its center. A smaller holding tank communicates with the pool through a wooden gate. Three hemispherical underwater viewing ports allow surveillance of the entire pool.

Net barriers were placed at various points along the pool wall to construct a circular enclosure or crowding chamber about 20 m in diameter in which porpoise were tested. The crowding chamber had two radial walls of netting that extended from the outer edge of the chamber to a central aluminum mast. One of the walls was stationary and was provided with escape openings of various dimensions. The other wall was movable and was used to drive the animals through the opening in the stationary wall. The movable wall pivoted on the central mast and was supported along the leading edge by an aluminum beam and on the distal end by a plastic float. The edge of the pool was marked at 1° intervals.

The walls were made of tuna purse-seine webbing (4¼-inch stretched mesh [10.8 cm] #42 thread knotted nylon). Flotation was provided by purse-seine-type corkline constructed of 6-inch diameter × 3½-inch (15 × 9 cm) sponge-plastic floats.

The basic escape opening was 18 ft (5.5 m) wide and 6 ft (1.8 m) deep. Flaps of purse-seine webbing were laced in, to variously decrease width to 10, 5, or 2½ ft (approximately 3.0, 1.5, or 0.8 m) and/or depth to 3½, 3, 2, 1, or ½ ft (approximately 1.1, 0.9, 0.6, or 0.2 m). For tests of response to a barrier across the opening at the water surface, a corkline constructed of hollow plastic floats (5 × 9 inch [13 × 23 cm], 4 per m) was strung across the top of the opening. In tests of response to barriers of acoustically low-reflective materials, a panel of 3⅜-inch (stretched) mesh (8.6 cm) #12 monofilament webbing, a panel of 0.38-mm-thick polyvinyl sheeting, or a panel of 1.04-mm-thick polyvinyl sheeting, was laced into the opening.

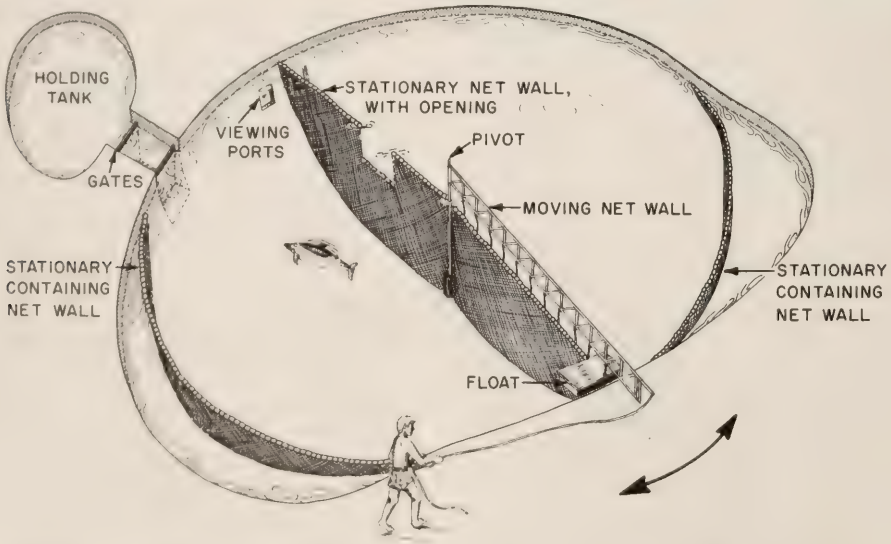

FIGURE 1.—Crowding chamber. Largest diameter of pool is 80 feet. Sketch not drawn to scale.

Acoustical tests carried out by the Naval Undersea Research and Development Center, San Diego, Calif., on plastic sheeting of similar thicknesses indicated effective acoustic transparency in the range of porpoise emanations (personal communication from W. E. Evans).

PROCEDURES

The moving wall was rotated around the center mast at a rate sufficient to completely close the chamber in about 4 min. An attempt was made to maintain a constant rate of rotation. Time required for an animal to escape from the chamber was recorded in seconds with a stopwatch, and position of the moving wall at time of escape was recorded in degrees. The reading in degrees was later used to calculate surface area remaining in the crowding chamber at time of escape. The wall was rotated alternately in clockwise and counterclockwise directions. After escape of an animal, the moving net wall was rotated until it was against the stationary wall, and the two radial nets remained together until the beginning of the next trial. Trails were spaced initially at 15-min intervals, to allow time for changing the escape opening. After our proficiency in altering the opening increased, the interval was decreased to 10 min.

Two major types of experimental design were used: (1) a long series of trials alternating two treatments and (2) a series of blocks of consecutive trials of various treatments. In some experiments, the two approaches were combined to yield a factorial design testing simultaneously the effects of variation in two or three of the factors of width, depth, and presence or absence of corkline, monofilament, or polyvinyl barriers. In some tests of the monofilament and polyvinyl panels, the animal was subjected to a single trial with the panel after a series of learning trials without the panel or at the beginning or conclusion of an experiment involving other variables. The design of these experiments is referred to below as "single trial." The results of the first series of experiments (Waimea I, II, and III; see Table 2) using the alternating trials design indicated a probable influence by the direction of rotation of the net wall or by stage of practice effect. The small number of trials in each experiment precluded complete randomization, but the treatments in subsequent experiments were staggered to offset the effect of direction of rotation. A typical sequence of trials was: *a, b, a, b, a, a, b, a, b, b;* where *a* and *b* were different treatments, and rotation in the first trial was clockwise, in the second counterclockwise, and so on in alternating fashion. In this manner, an equal number of clockwise and counterclockwise trials was assured for each treatment.

TABLE 2.—Preliminary experiments with trained porpoise.

Porpoise	Experiment	Variables tested	Design	Number of trials
Waimea	I	Width	Alternating trials	20
	II	Width	Alternating trials	20
	III	Depth, corkline	Factorial	26
	IV	Monofilament panel	Single trial	14
Nani	I	Depth	Alternating trials	20
	II: trials 1-19	Width, depth	Factorial	19
	trial 20	Corkline	Single trial	1
	III: trial 1	Corkline	Single trial	1
	trials 2-16	Depth	Block	16
	trials 17-30	Depth, monofilament panel	Factorial	14
Nohea	I	Depth	Alternating trials	22
	II	Depth	Block	36
	III: trials 1-36	Width	Block	36
	trials 37-44	Depth	Alternating trials	8
	trial 45	Monofilament panel	Single trial	1
	IV	Width, depth, corkline	Factorial	32
	V: trials 1-8	Depth	Alternating trials	8
	trial 9	Thin polyvinyl panel	Single trial	1
	VI: trials 1-8	Depth	Alternating trials	8
	trial 9	Thick polyvinyl panel	Single trial	1

The remaining surface area between the advancing net wall and the stationary wall at the time of escape was used as a criterion of the animals' readiness to escape. This index was the inverse of latency, since the smaller the area that remained when the animal escaped the longer would be the latency. Although we measured latency in seconds, we felt the net position was the preferable measurement because the rate of net movement was imprecise, whereas the actual stimulus for escape, the reduction in the swimming area, could be measured relatively accurately. In presentation of the data, the logarithm (to base 10) of the remaining area at the time of escape is plotted on trial number.

Because procedures and plans were modified during the course of the experiments, results and interpretation are combined in the presentation of the results.

PRELIMINARY EXPERIMENTS WITH TRAINED PORPOISE

We anticipated that the behavior of the porpoise would change rapidly during the course of the experiments; thus, to avoid wastage of the naiveté of the limited and expensive supply of untrained animals, we conducted a series of preliminary experiments with three trained porpoise (Table 2, Figures 2-4).

WIDTH OF OPENING

The effect of the width of the opening on the escape behavior of the three trained porpoise was first tested by presenting on alternate trials an escape route of standard width, 5.5 m, and one either 3.1 or 3.8 m wide. In Waimea (Figures 2-I and II) and Nohea (Figure 4-IV) there was some evidence that the porpoise escaped sooner when the wider escape route was used but not in Nani (Figure 3-II). We felt this was probably an artifact of experimental design as described above and consequently we considered only the data from the block experiments for evaluating effects of width on the trained porpoise. To determine the width of opening that would influence performance, Nohea was tested over six

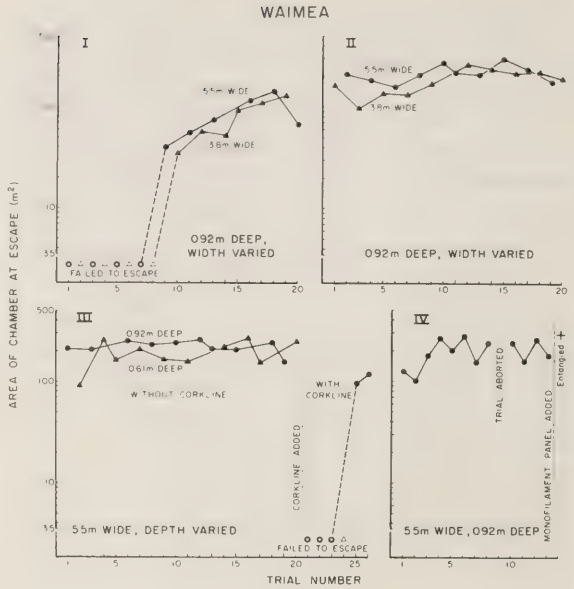

FIGURE 2.—Results of experiments with trained porpoise Waimea. Each plot summarizes one day's continuous experimentation, as follows: I. May 21, II. May 22, III. May 23, IV. May 25, 1970.

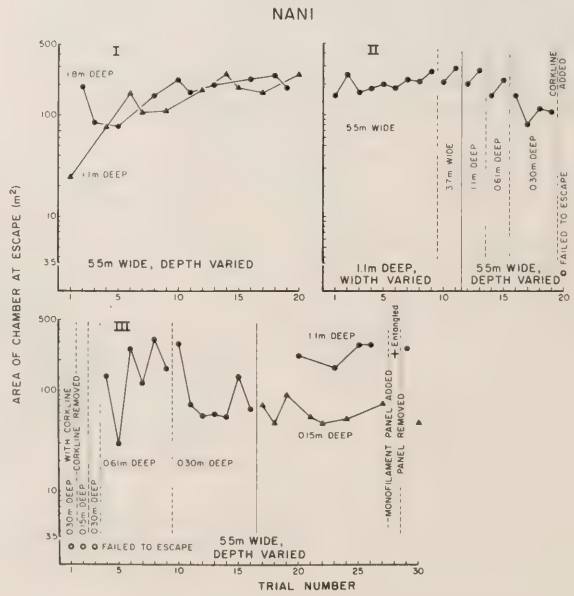

FIGURE 3.—Results of experiments with trained porpoise Nani. I. May 26, II. May 27, III. May 28, 1970.

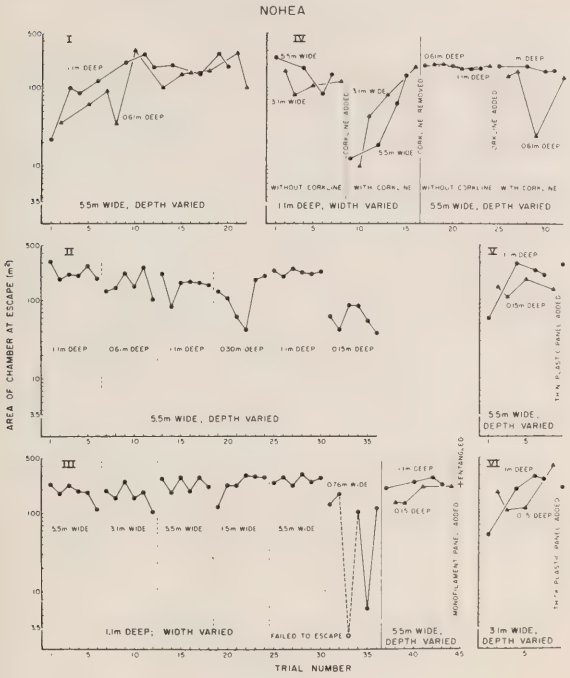

FIGURE 4.—Results of experiments with trained porpoise Nohea. I. May 30, II. May 31, III. June 1, IV. June 21, V. June 28, VI. June 29, 1970.

blocks of six trials each (Figure 4-III). The width of the escape route was 3.1 m in the second, 1.5 m in the fourth, and 0.76 m in the sixth block of experimental trials, with interspersed blocks of trials at 5.5 m. A significant decrease in performance occurred only when the escape opening was narrowed to 0.76 m. In one trial at 0.76 m the animal refused to leave the crowding chamber and had to be extricated from the webbing. In others, the porpoise exhaled air and sank passively to the bottom of the pool and did not move even when the chamber was completely closed. Exhalation of air and sinking to the bottom was a pattern that appeared in other porpoise in other experiments and was accompanied by failure to escape.

Our tentative conclusion was that the width of the opening was not a significant variable in the block experiments if it exceeded about 1.5 m.

DEPTH OF OPENING

We determined the effect of the depth of the escape route by varying depth of the hole from 1.8 m to 0.15 m while maintaining the standard hole width of 5.5 m. We will describe the results for each porpoise separately since the experiments were different for each animal.

Waimea failed in the first eight trials to escape through an opening 0.92 m deep (Figure 2-I). Performance improved thereafter to a plateau that was maintained throughout a subsequent identical experiment the next day, throughout a series of alternating trials with 0.92-m- and 0.61-m-deep openings on the third day of the experiments, and in a fourth experiment (Waimea IV) 2 days later with a 0.92-m-deep opening.

Nani showed no difference in response after the first two trials with openings 1.8 m and 1.1 m deep (Figure 3-I). High performance continued through a series of trials with a 1.1-m-deep opening, but dropped in blocks of trials of 0.61-m- and 0.30-m-deep openings (II). In subsequent experiments Nani failed to escape twice when openings 0.15 m and 0.30 m deep were used and performed erratically in blocks of trials with openings 0.61 m and 0.30 m deep (III). After seven trials with the 0.30-m opening, no failures was experienced in seven trials with a 0.15-m opening, but the animal escaped consistently earlier (larger remaining area) when the 1.1-m-deep opening was used.

Nohea escaped earlier when the hole was 1.1 m than when it was 0.61 m deep in 14 of the first 16 trials of an alternating series (Figure 4-I). In a subsequent series of blocks of trials at decreasing depths (II), a pronounced drop in performance occurred at depths of 1 ft and 5 ft. The following day's performance remained at a high level except when a corkline was strung across the opening (IV).

Our tentative interpretation of the above results was that a critical depth of opening lay near 1 m: 11 failures to escape occurred at 0.92 m or shallower; none occurred with openings 1.1 m deep or deeper; and performance was even more adversely affected by further decreasing the depth of the opening. We also concluded that the results of the first few trials for each ani-

mal were of most importance in predicting the probable response of naive wild porpoise, as the animals were able quickly to achieve high levels of performance even at very shallow depths.

CORKLINE

A corkline across the top of the opening caused Waimea (III) and Nani (II) to fail on initial trials, and greatly affected the performance of Nohea (IV). Waimea, after four failures, overcame reluctance to pass through an opening with a corkline at the surface and reachieved a high level of performance. An interaction between the corkline and depth of opening was apparent in the factorial experiment with Nohea. Initial trials with the corkline (second block) produced a temporary drop in performance with a 1.1-m-deep opening. In the fourth block, the corkline was again inserted, and performance dropped at 0.61 m depth but not at 1.1 m.

MONOFILAMENT PANEL

When the panel of nylon monofilament webbing was inserted into the opening (1.1 m deep) after a series of trials in which performance was consistently high, Waimea (IV), Nani (III), and Nohea (III) swam into the webbing as if it did not exist. Performance in subsequent trials without the panel was not affected (Nani III). Upon hitting the webbing, the porpoise became entangled and had to be extricated by a diver.

POLYVINYL PANEL

In the two single trials with a panel of clear polyvinyl sheeting inserted in the opening, Nohea (V and VI) hit the panel and slid over the top as it buckled. No difference was noted in behavior in these trials from that in trials in which the panel was absent.

During these experiments Nohea in several trials passed back and forth through the opening two or three times after the initial escape, while the net wall was being closed. The values for the surface area index shown in the figure are for the first passage. The incidence of such behavior throughout the course of all the experiments occurred only after considerable experience with a particular net configuration. In most cases, only one or two double "escapes" occurred during an experiment.

EXPERIMENTS WITH NAIVE PORPOISE

Eleven experiments were conducted with the naive porpoise (Table 3, Figures 5 and 6). The first naive animal, Westward, was captured on June 12, 1970, and after a relatively short handling period was placed in Bateson's Bay. Her swimming behavior during the first 5 days of captivity was unlike that of the trained porpoise. The trained porpoise continually swam about the tank during and between experiments, diving and "porpoising," and spinning. Westward, on

TABLE 3.—Experiments with naive porpoise.

Porpoise	Experiment	Variables tested	Design	Number of trials
Westward	I	Depth	Alternating trials	20
	II	Depth	Alternating trials	20
	III	Depth	Block	36
	IV: trials 1-40	Depth, width, corkline	Factorial	40
	trial 41	Monofilament panel	Single trial	41
	V	Width	Block	36
	VI: trials 1-10	Depth, thin polyvinyl panel	Factorial	10
	trials 11-15	Thick polyvinyl panel	Block	5
Moana	I	Depth	Alternating trials	11
	II	Depth	Alternating trials	20
	III	Width	Block	36
	IV	Depth	Block	24
	V: trials 1-12	Depth	Block	12
	trials 13-25	Width, corkline	Factorial	13

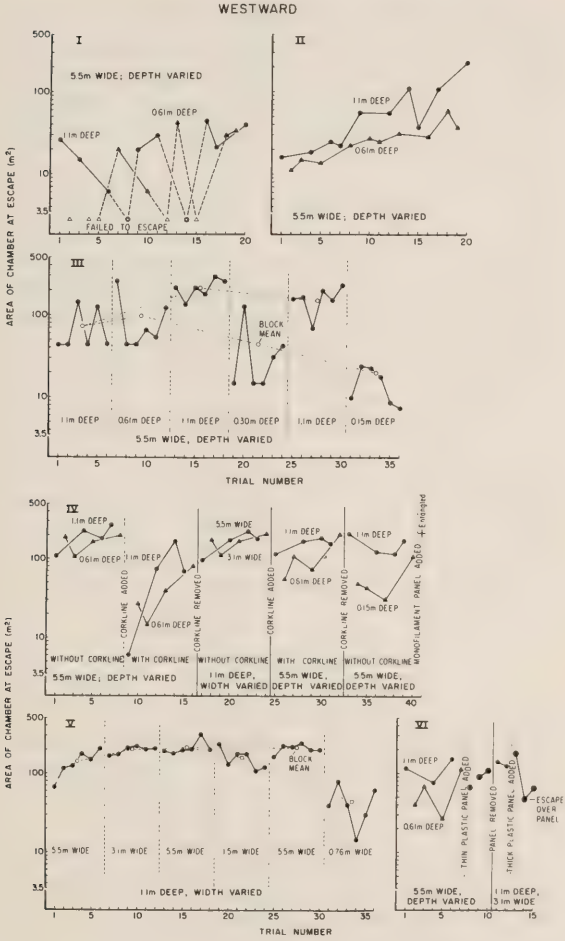

FIGURE 5.—Results of experiments with naive porpoise Westward. I. June 12, II. June 22, III. June 24, IV. June 25, V. June 26, VI. June 29, 1970.

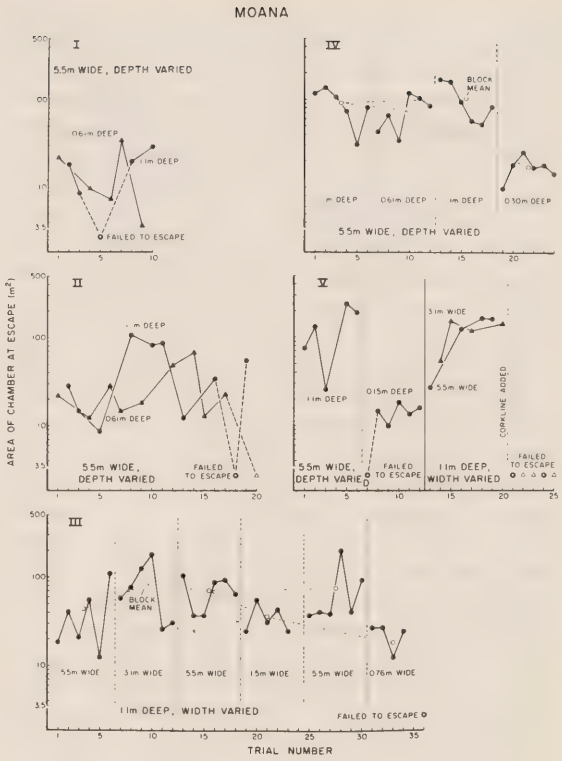

FIGURE 6.—Results of experiments with naive porpoise Moana. I. July 10, II. July 11, III. July 12, IV. July 13, V. July 15, 1970.

the other hand, remained at the surface in a near-upright position with blowhole exposed and rostrum submerged, swimming very slowly with slow, low-amplitude beats of the posterior half of the body. Her head bobbed up and down slightly as she swam. Opinion among the animal-training staff of the Oceanic Institute as to the cause of this behavior was divided; some believed the animal to be in shock, perhaps even moribund, others believed the behavior to indicate extreme fright. The first experiment was carried out the day after capture. Subsequently Westward's behavior slowly changed, until 5 days later on June 17 it was indistinguishable from that of the trained porpoise. The remainder of the Westward experiments were carried out after June 17.

Moana, the second naive porpoise, was captured on July 9, 1970. When placed in Bateson's Bay, she exhibited the same behavior as Westward, but to a lesser extent. Periods of surface swimming in a semiupright position, but without head-bobbing, were interspersed with periods of normal porpoising and diving. During the first experiment she swam slowly at the surface in the diagonal posture but during the second and subsequent experiments, her behavior was similar to that of the trained animals.

DEPTH OF OPENING

In the first few trials (Figure 5-I) a marked difference existed in the response of Westward to an opening 1.1 m deep and one 0.61 m deep. The animal swam slowly at the surface, circling or moving back and forth in the chamber. When the opening was 1.1 m deep, she moved slowly through the opening just as the moving wall closed. When the opening was 0.61 m deep, she moved past or circled slowly in front of the opening and then dove and entangled herself in the webbing of the moving wall. In the sixth trial, her behavior became more varied; she swam in tight circles beneath the surface and attempted to pass between the end of the moving wall and the periphery of the chamber before passing through the opening, after which she slapped her tail against the water surface. Behavior in subsequent trials became increasingly erratic. In trial 13 she darted through the opening rather than moving through slowly as in the previous trials. In trial 14, she tried again to squeeze past the moving wall and became lodged in the narrow opening. In trial 15, she assumed a position across the corkline of the moving wall, half in and half out of the chamber, and remained there until removed. In the remaining trials, she moved rapidly through the opening, and in the last two, she assumed a horizontal attitude similar to that usually taken by the trained porpoise and stopped bobbing her head but still kept her blowhole above the surface.

An identical experiment (II) of alternating trials was carried out 5 days later, after all traces of the slow surface-swimming and head-bobbing behavior had disappeared. Performance was consistently higher with the 1.1-m opening. The effect of depth is clearly seen in the results of a block-design experiment for Westward (III).

The second naive porpoise, Moana, a smaller and presumably younger animal than Westward, achieved a higher rate of successful passage in the first depth experiment (Figure 6-I). She failed only once, with the 1.1-m-deep opening. In the second depth experiment (II) her performance was extremely variable compared to that of Westward, and no relation between depth and success rate existed. In two trials (18 and 20) while swimming in tight circles near the apex of the chamber, she snagged her flipper in the webbing and had to be extricated. In later block-design experiments (V and IV) the effect of depth was evident as it was for Westward.

WIDTH OF OPENING

Results of block-design experiments testing the effect of width of opening for Westward (Figure 5-V) and for Moana (III) were similar to those for the trained porpoise (Nohea), but an effect was discernible at widths of 1.5 m.

As with the other experiments, performance of Westward was higher and more stable than that of Moana. Westward began to pass through the opening two or three times during a single trial. The frequency of multiple "escapes" was higher for the 5.5-m-wide opening than for the narrower openings (Table 4).

CORKLINE

Insertion of a corkline at the surface across the top of the opening sharply affected the performance of Westward (IV) and Moana (V). The performance of Moana showed the greatest effect. After a series of preparatory trials, Moana failed to pass through the opening in five straight trials with the corkline. In each trial she laid the anterior part of her body across the corkline and remained there until removed. In the block-design experiments with Westward (IV), the second block of trials with a corkline produced a smaller drop in performance than did the first, with the 0.61-m-deep opening only, demonstrating as for the trained porpoise (Nohea IV, Figure 4) an interaction between depth and presence or absence of a barrier at the surface.

TABLE 4.—Multiple escapes of Westward.

Width of opening in block of six trials	Number of double escapes	Number of triple escapes
m		
5.5	0	0
3.1	1	0
5.5	2	2
1.5	1	0
5.5	2	0
0.76	0	0

MONOFILAMENT AND POLYVINYL PANELS

When the monofilament panel was inserted into the 1.1-m-deep opening at the end of a series of depth trials, Westward (IV) "got up a full head of steam and plowed into the monofilament" (extracted from field notes of W. Wasden) and became entangled. Insertion of polyvinyl panels produced similar results in multiple trials; Westward (VI) in each trial hit the panel and slid over it and out of the chamber. There was nothing in the behavior of the porpoise to indicate that they recognized the presence of the panels.

DISCUSSION AND CONCLUSIONS

The swimming behavior of the naive porpoise Westward and, to a lesser extent, of Moana, the first few days after capture was very similar to that of porpoise (*Stenella* spp.) in tuna purse seines as observed by one of us (Perrin) off Central America. A typical "failure to escape" episode is illustrated for Moana in Figure 7. Immediately after a purse-seine net has been set, when the diameter of the encircled area is greatest (approximately 250 m), the porpoise swim about quite rapidly in small tight groups of a dozen or so individuals, the members of a group diving and surfacing together (Figure 8). As the net is hauled and the area enclosed becomes smaller, especially after the backing down operation (see Perrin, 1969), the porpoise congregate and raft near the center of the enclosure and mill very slowly, holding their bodies in a semiupright position with blowhole exposed and rostrum at or slightly below the surface (Figure 9). At this point, individual animals can be seen to leave the group and dive. When the net has been completely hauled, animals are often found with their snouts entangled in the webbing several meters below the corkline.

Although the head bobbing exhibited by Westward was not observed in the purse-seine situation, the similarities in behavior between freshly captured animals and those captured in a purse seine were striking. In both cases the animals did not display normal motor patterns; they rested or swam at abnormally slow speeds, and this behavior was often ended by a rapid dive beneath the surface with no noticeable change in behavior preceding the act. The principal characteristics of this behavior, the inhibition of activity in a fear-inducing environment, resembled fear responses described for many other vertebrates and frequently classified as an immobility or freezing response (Ratner and Thompson, 1960; Hinde, 1970). Hogan (1965, 1966) suggested that withdrawal and immobility are separate, mutually inhibitory systems. If this view is correct, then driving porpoise through an escape route in the purse seine would not be successful once the animals began to show the immobility response, because withdrawal would be inhibited. Under these circumstances the additional fear stimulus associated with driving might be the catalyst for the rapid dive to escape, which results in entanglement. Driving may have to be carried out before immobility begins. Once the animals became immobile the only strategy may be to pull the net out from beneath them as is currently done during the "backing down operation" (Perrin, 1969).

That the behavior of Westward and Moana evolved into more typical behavior during the course of a single experiment also supports the notion that their unusual behavior was caused by the circumstance of captivity rather than ill health.

Our conclusions with respect to projected design of a rescue gate for removing porpoise from a purse seine during fishing operations were:

1. The gate should be sufficiently wide so that when the perimeter of the net circle buckles after pursing, the width does not become less than 1.5 m. Considering the equivocal results of the experiments for openings wider than 1.5 m, the opening should be as wide as practically possible.

2. Depth of the opening should be not less than 1 m and as deep as it is possible to make it without causing loss of the fish in the net.

3. There should be no line, corkline, or other barrier across the opening at the surface.

4. A self-actuating release port that will open when struck by a porpoise swimming into it

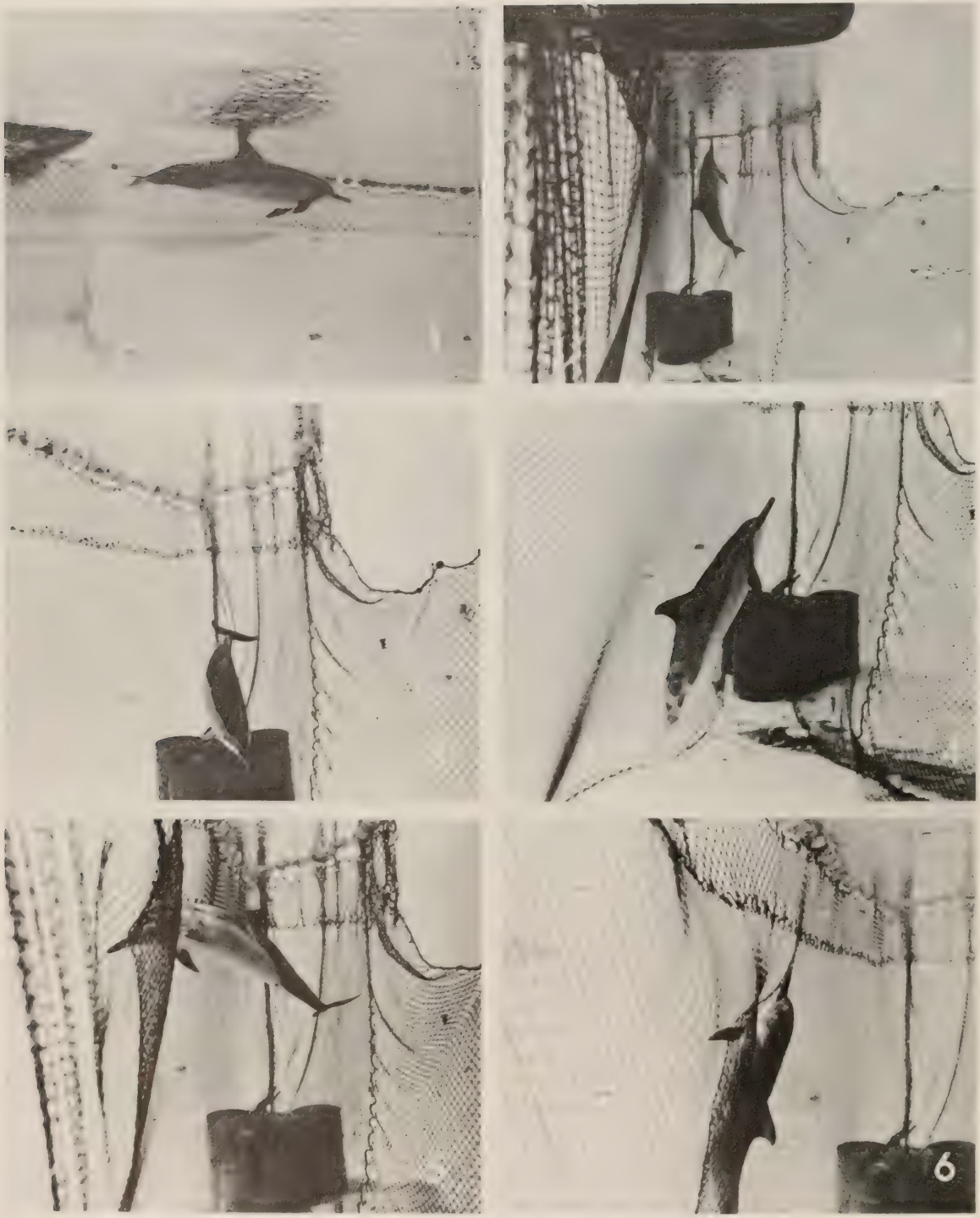
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FIGURE 7.—Typical "failure to escape" episode. Moana (1) patrols moving wall at beginning of trial, then (2) takes up position at apex of chamber and remains there for most of trial, in vertical attitude. As chamber nears closure Moana dives (3), orients toward opening (4), and turns and swims into moving wall (5), becoming entangled (6).

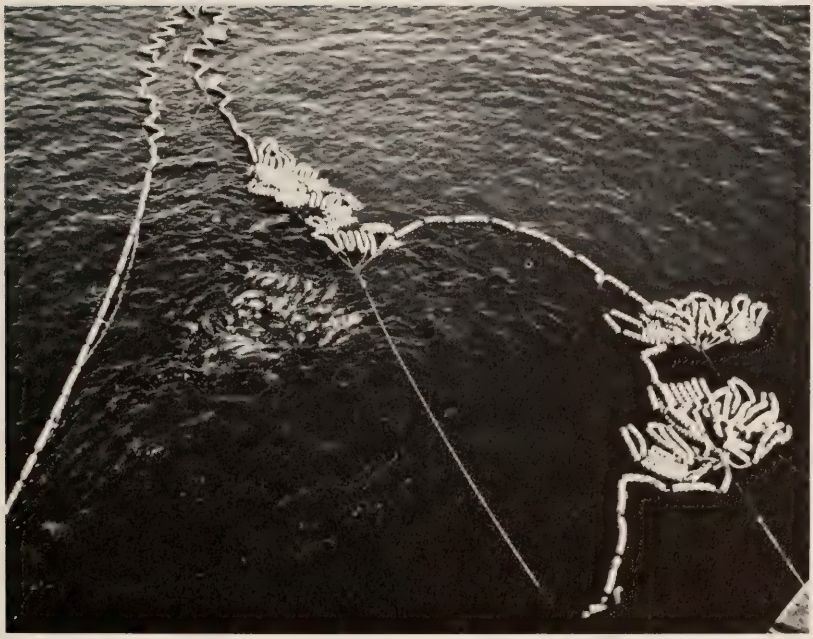

FIGURE 8.—Porpoise (*Stenella graffmani*) in tuna purse seine at beginning of set, when net is at near-maximum diameter. Animals are circling and diving in groups of a dozen or so individuals.

FIGURE 9.—Porpoise in purse seine, after most of net has been taken aboard. Animals are "rafting" in compact group, each maintaining approximately vertical attitude, with blowhole exposed and dorsal fin submerged. Large fish underwater in foreground are yellowfin tuna.

might be feasible if constructed of acoustically transparent materials, providing that it were so constructed that the fish in the net would not also use it.

5. It is to be expected that great difficulty will be encountered in inducing wild porpoise to pass through an opening in the perimeter of a purse-seine enclosure.

ACKNOWLEDGMENTS

We thank the Oceanic Institute and its Director, Dr. Kenneth Norris, for providing the facilities and the porpoise used in this study. William Wasden, National Marine Fisheries Service, Honolulu, Hawaii, assisted in all phases of the study, and porpoise trainers Ingrid Kang, Sea Life Park, and Scott Rutherford, Oceanic Institute, provided assistance and advice during the course of the experiments.

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METHODS FOR TAGGING SMALL CETACEANS

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ABSTRACT

Four types of tags have been used on four species of delphinids. These include a circular plastic button tag that is attached to the dorsal fin by a nylon bolt, a highly visible dart-type spaghetti tag that is placed near the base of the dorsal fin, a radio transmitter tag, and a freeze brand.

Use of button tags has been discontinued due to high shedding rate. The dart-type spaghetti tag has proved best for tagging large numbers of animals without capturing them. The radio tag provides very detailed information on behavior and movements, while freeze branding provides a permanent mark, though both require capturing the animal.

The importance of marking commercially valuable species of whales (primarily the larger baleen whales and the sperm whale) has long been recognized. Since their development in the mid-1920's, "Discovery-type" tags have been used to mark large numbers of these animals (Rayner, 1940; Brown, 1962; Clark 1962). Returns from these tags have provided valuable information on the species' distribution, migration, and abundance and on such basic aspects of their biology as relative growth rates and the timing of the events in their lives (Mackintosh, 1965).

The relationship of several small delphinid species to commercial fish populations and the potential of these cetaceans as a major economic resource has renewed interest in their stocks during the last decade (Perrin, 1970). Early attempts to study these populations in the wild have been hampered by the difficulty of positively identifying an animal or a population from one encounter to the next. Therefore, development of a reasonable method for marking these animals for identification would facilitate studies of their life histories.

Although several investigators have tried tagging small cetaceans, only three have had even moderate success. In a program conducted by the Oceanic Institute, Oahu, Hawaii, plastic cattle eartags were placed on two *Steno bredanensis* and one *Stenella attenuata* (Evans, 1967). This program was continued by Norris and Pryor (1970), and at least one of the tags was still on a *Stenella attenuata* when it was resighted after 3½ years.

Sergeant and Brodie (1969) tagged 812 belugas, *Delphinapterus leucas*, in Hudson Bay, Canada, over a 2-year period. Six hundred and ninety-four of these animals were tagged with a spaghetti tag originally designed by Mather (1963) for use in tagging pelagic fishes and manufactured by Floy Tag Company,[4] Seattle, Wash. The remaining 118 belugas were tagged with Petersen disc tags, similar to the button tags we used. Of the 812 animals tagged, 2 with spaghetti tags were recovered by the beluga fishery. A third spaghetti tag was observed in a live animal temporarily stranded by the ebbing tide 1 year after the original tagging.

Perrin and Orange (1971) tagged 218 *Stenella* spp. in 1969 and approximately 1,000 in 1970 in the eastern tropical Pacific with spaghetti-type dart tags. Five tags have been recovered; maximum time at liberty was 138 days (916 km net movement).

Since 1968, personnel of the Naval Undersea Research and Development Center's Marine Bioscience Division at San Diego, Calif., have been

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[4] Reference to commercial products does not imply endorsement by the National Marine Fisheries Service.

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investigating the distribution and biology of several odontocete cetaceans off the southern California coast. In order to delineate migration routes and to keep track of local herds of the common dolphin, *Delphinus delphis* auctt., a tagging program was initiated. During the same period, a tagging program was also initiated for *Tursiops truncatus* on the west coast of Florida. The special problems associated with tagging odontocete cetaceans required the modification of old and the development of new tagging techniques.

This paper discusses the relative merits of the four marking methods used by our laboratory. In addition, it presents some preliminary results of the program in order to substantiate the utility of the various methods.

METHODS AND RESULTS

We have used modified dart-type vinyl spaghetti tags (Floy Manufacturing Company) on four species of Eastern Pacific delphinids in an area from Point Conception, Calif., to Cabo San Lucas, Baja California, Mexico, and throughout the Gulf of California. Our original spaghetti tags were 5 mm in diameter by 17 cm long. In order to increase visibility and flow characteristics of the tag, we increased the length to 30 cm (Figure 1). Using the modified tag, we have marked 240 *D. delphis*, 10 *Lagenorhynchus obliquidens*, 8 *Tursiops gilli* auctt., and 13 *Stenella graffmani* to date (July 1971). The animals were all tagged at the anterior insertion of the dorsal fin while they were surfing on the bow pressure wave. Several dolphins were observed to continue riding the bow pressure wave after being tagged, so the tagging process apparently did not affect their normal behavior.

A *T. gilli* auctt., tagged on 27 October 1970, off Magdalena Bay, Baja California, was recovered by an American tuna boat off Manzainillo, Mexico, on 22 January 1971. The animal had covered at least 816 km between the time of tagging and the time of capture, a period of just less than 3 months.

Three *D. delphis* bearing spaghetti tags have been observed swimming in the vicinity of the Coronado Islands near San Diego, Calif., and at least one spaghetti-tagged *D. delphis* has been sighted off Magdalena Bay, Baja California. Each of these animals was known to have been carrying the tag for from 2 weeks to several months.

Circular plastic "button" tags (10 cm diam) (Figure 2) were through-bolted to the dorsal fins of 46 *D. delphis* and 6 *L. obliquidens* between 1967 and 1970. These tags are similar to those employed by Norris and Pryor (1970) in Hawaii, but are larger to make them more easily spotted. Button tags were attached to animals captured off the southern California coast, or near Cedros

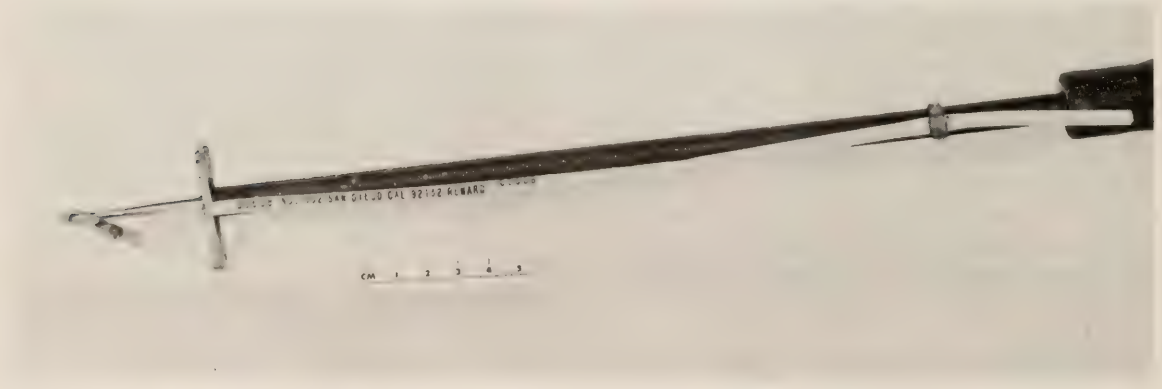

FIGURE 1.—The dart-type spaghetti tag in place on the tagging apparatus.

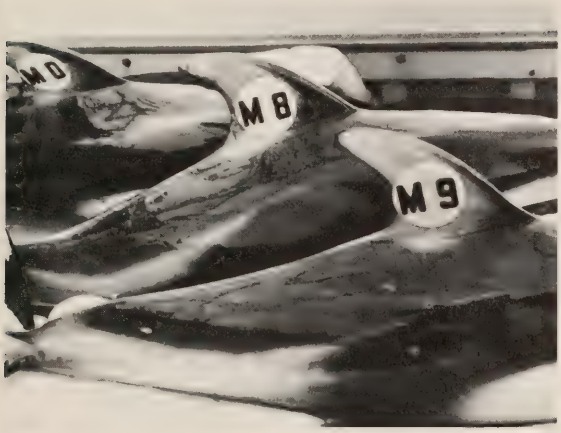

FIGURE 2.—Three *Lagenorhynchus obliquidens* with the plastic button tag, just prior to release.

Island, Baja California. Two of the *L. obliquidens* tagged in 1969 were resighted almost 1 year later, and a *D. delphis* tagged in 1968 was resighted 21 months later.

Twenty-four *T. truncatus* were tagged with the button tags near Sarasota, Fla., from August 1970 through September 1971. Animals bearing tags have been resighted several times.

The third and most successful short-term tag is the radio transmitter tag with which at least four species of small cetaceans have been successfully marked to date (Evans, in press, Martin, Evans, and Bowers, 1971). The original package used in these studies was a 27 mHz (11 m) transmitter and antenna housed in a waterproof envelope which is attached to the dorsal fin of a dolphin or a small whale by means of a spring-loaded corrosible link. The link dissolves and releases in 30 days, allowing the package to slip off the animal.

These early radio beacons, designed for short-term transmission (30-60 days), weighed up to 900 g, and though they proved especially useful in studying the detailed movements of *D. delphis* in the waters off San Diego, Calif., their size, cost, and relatively short transmission time made them unacceptable for long-term monitoring of herd movements.

To meet this need, a new lightweight radio tag (170 g) with a 9-12 month transmitter life was developed. This tag combines the advantages of a radio beacon and a button tag in that it continues to serve as a color coded marked even after it no longer transmits (Figure 3). Furthermore, the new radio tag is available commercially at less than 10% of the cost of the 900/gm transmitters.

FIGURE 3.—The lightweight (170 g) radio tag.

The fourth method, freeze branding, consists of applying a supercooled branding iron, usually copper, to the epidermal surface of the dolphin for 5-30 sec. Evidence from freeze branding cattle indicates that the branding process is painless to the animal and has no lasting effect other than leaving a permanent mark (Farrell, Laisner, and Russell, 1969). Though evidence of the branding usually becomes indistinct shortly after application, after about 2 months the animal will display a highly legible brand (Figure 4). We have used this method on eight wild *T. truncatus* near Sarasota in conjunction with either a button tag or a spaghetti tag. The number on a freeze branded animal was clearly visible, from a distance of 40 yards, when the animal was resighted 10 weeks after tagging.

FIGURE 4.—A *Tursiops truncatus* with the freeze brand on the dorsal fin.

DISCUSSION

We have discontinued use of the button tag in favor of the spaghetti and radio tags. Incidence of loss of button tags from animals has been exceptionally high among the *T. truncatus* around Sarasota, and the few resightings of button-tagged dolphins off southern California lead us to believe that button tag loss is high in this area also. A major disadvantage of the button tag is that the animal must be captured in order to be tagged. The spaghetti tag, on the other hand, is normally placed in the animal while it is free swimming and thus does not require capture. Using this method we have placed over 50 spaghetti tags in one herd of *D. delphis* in less than 2 hr. When spaghetti tags are placed in the fibrous tissue at the insertion of the dorsal fin, incidence of tag loss appears to be lower for spaghetti tags than for the button tags (Nishiwaki, Nakajima, and Tobayama, 1966). In either case, the numbered information on the tag is so small that it cannot be read on a moving animal at sea. Unless the spaghetti tags are color-coded, resighting at sea can give no information on the original tagging location. Spaghetti tags may also be placed in an animal that has been captured.

The radio tags can be placed only on captured animals but provide very detailed information concerning exact movement and diving patterns of the animal.

While freeze branding involves capture of the animal, it appears to provide permanent and highly legible identification of cetaceans. Tomilin (1962) reported taking a Black Sea *D. delphis* in 1953 which bore a brand posterior to the eye. The brand was quite legible and contained numbered information. The source and nature of the brand were not known. In the future, we plan to freeze brand all the dolphins we capture for radio tagging and to continue to use the spaghetti tags for free-swimming delphinids.

An advertisement was placed in the July issue of *National Fisherman* requesting that any information on sightings of tagged delphinids in the Eastern Pacific be forwarded to the Marine Bioscience Division of the Naval Undersea R & D Center, San Diego, Calif. (Evans, Leatherwood, and Hall, 1971). Copies of this advertisement have been placed at sportfish landings and commercial docks from Santa Barbara to San Diego, Calif.

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A REVIEW OF THE LANTERNFISH GENUS *Taaningichthys* (FAMILY MYCTOPHIDAE) WITH THE DESCRIPTION OF A NEW SPECIES

BRENT DAVY[1]

ABSTRACT

The genus *Taaningichthys* includes three known species, one of which is here described as new.

The species of the genus *Taaningichthys* do not appear to perform daily vertical migrations. Evidence indicates vertical stratification of juveniles and adults.

Although photophores and lateral line are reduced, the species of *Taaningichthys* possess very large eyes which may be related to capture of luminescent prey.

Otoliths of all three species have been examined and found to be taxonomically important.

Bolin (1959) erected the genus *Taaningichthys* to include two species, *T. bathyphilus* and *T. minimus*, previously placed in the genus *Lampadena* by Tåning (1928). The main characters which distinguish *Taaningichthys* from *Lampadena* are: (1) the origin of the dorsal fin in *Taaningichthys* is clearly behind the base of the pelvic fins; (2) the development in *Taaningichthys* of a crescent of white tissue[2] on the posterior half of the iris, although a similar white (luminous?) crescent is present on the dorsal portion of the iris in *Lampadena chavesi* (Nafpaktitis and Paxton, 1968); (3) the presence of a single SAO, or none, in *Taaningichthys* (always three SAO in *Lampadena*); (4) reduced dentition and lateral line in *Taaningichthys*.

Taaningichthys may be distinguished from all other myctophid genera by the combination of the white crescent of tissue on the posterior half of the iris, the undivided luminescent caudal glands, and the single or altogether absent SAO.

Berry and Perkins (1966) reported what they thought to be a third form of *Taaningichthys* apparently without photophores. Following the capture of a number of specimens of this form by the RV *Velero IV* of the University of Southern California and the examination of considerable material made available to me by numerous institutions around the world, I felt that a review of the genus was appropriate.

MATERIALS AND METHODS

Members of the genus *Taaningichthys* are deep-dwelling, fragile myctophids, easily damaged by the net. Scales are readily lost, and damage to the bones of the snout, upper jaw, and operculum is very common. Consequently, measurement of jaw, head, and snout length is often very difficult if at all possible. The following measurements were taken on the best preserved specimens: Eye diameter (ED)—horizontal distance across the orbit; jaw length (JL)—length of premaxillary; predorsal (Pre D)—anterior tip of premaxillary to base of anteriormost ray of dorsal fin; preventral (Pre V)—anterior tip of premaxillary to base of anteriormost ray of ventral fin; preanal (Pre A)—anterior tip of premaxillary to base of anteriormost ray of anal fin; prepectoral (Pre P)—anterior tip of premaxillary to base of anteriormost ray of pectoral fin; preadipose (Pre Ad)—anterior tip of premaxillary to posterior end of base of adipose fin; length of supra- and infracaudal luminous glands—length of exposed luminous tissue only; anal-infracaudal distance—anterior tip of

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[2] This tissue is not visible until some time after preservation and is hardly distinguishable in specimens initially frozen and then preserved.

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infracaudal gland to end of base of anal fin. Sizes of specimens are given in standard lengths (SL) only.

Terminology of body photophores follows that of Bolin (1939). Unless otherwise specified, the term photophore refers to the primary body photophore.

Otoliths were measured with an eyepiece micrometer as follows: Length (OL)—the greatest length parallel to the sulcus; height (OH)—greatest height perpendicular to the sulcus. Following measurements, otoliths were lightly smeared with graphite to bring out detail and then photographed. Otolith terminology follows that of Frizzell and Dante (1965).

Female specimens were considered gravid when eggs included oil globules and completely filled the oviduct.

Most specimens examined were captured with open nets and depth sampled is here considered as the maximum depth reached by the net (appendix).

Counts of procurrent caudal rays are given as dorsal + ventral.

KEY TO THE SPECIES OF THE GENUS *Taaningichthys*

1a. VO 8-10; AO 5-7 + 4-6, total 9-13; Pol directly below or anterior to base of adipose fin; Prc_1-Prc_2 interspace equal to or greater than two photophore diameters; as many as five pairs of broad-based, hooklike teeth on dentary near symphysis ..... *T. minimus* (Tåning, 1928)

1b. VO, if present, 3-5; AO, if present, 1-4 + 1-2, total 2-5; Pol, if present, clearly behind base of adipose fin; Prc_1-Prc_2, if present, interspace equal to, or less than, one photophore diameter; no broad-based, hooklike teeth on dentary near symphysis 2

2a. Photophores present as in 1b above; anal-infracaudal distance half as long as length of infracaudal gland, or longer ..... *T. bathyphilus* (Tåning, 1928)

2b. Photophores absent; anal-infracaudal distance less than half length of infracaudal gland ..... *T. paurolychnus* n. sp.

FIGURE 1.—*Taaningichthys minimus* (Tåning); 46 mm, Ocean Acre stn. 7-21.

GENUS *Taaningichthys* Bolin

Taaningichthys minimus (Tåning, 1928)

Figures 1 and 2

Lampadena minima Tåning, 1928: 63; Parr, 1928: 154, Figure 37.

Lampadena (*Lampadena*) *minima* Fraser-Brunner, 1949: 1078, Figure.

Taaningichthys minimus Bolin, 1959: 26.

D 11-13; A 12-13 (11-14); P 15-17; V 8; gill rakers 4-5+1+11 (10-13), total 16-17 (15-18); VO 8-10; AO 5-7+4-6, total 9-13; Prc 2+1; vertebrae 40-41; procurrent caudal rays 8-10+8.

Mouth terminal, moderately large, JL about 1.5 in Pre P; maxillary slightly expanded posteriorly. Eye large, ED 2.2-3.4 in Pre P. Pterotic spine long and directed posteriorly. Opercular margin concave posterodorsally, slightly convex posteriorly. Pectoral fin long, reaching VO_6 or VO_7; its base about midway between ventral body margin and horizontal septum. Pre V 2-2.4 in SL. Pre D 1.9-2.3 in SL; end of base of dorsal fin clearly in advance of vent. Pre A 1.4-1.6 in SL. Anterior end of base of adipose fin on vertical through posterior end of base of anal fin; Pre Ad 1.2-1.3 in SL.

A band of dark pigment along anteroventral margin of orbit containing a series of light gray, triangular patches of tissue not present in the other two species.

Dn absent; Vn present between anterior margin of orbit and posteroventral margin of nasal rosette. PVO_1 on or behind vertical through upper end of base of pectoral fin and about midway between it and ventral margin of body; PVO_2 in front of middle of base of pectoral fin; a straight line through PVO_1 and PVO_2 passing in front of PLO. PLO about halfway between upper end of base of pectoral fin and horizontal septum. Five PO. VLO above base of pelvic fin, usually closer to horizontal septum than to ventral margin of body. Last VO usually slightly elevated. SAO 1-2 photophore diameters below horizontal septum, directly above vent. AO level. AO series overlaps anterior end of infracaudal gland. Pol directly below or in advance of base of adipose fin, 1-2 photophore

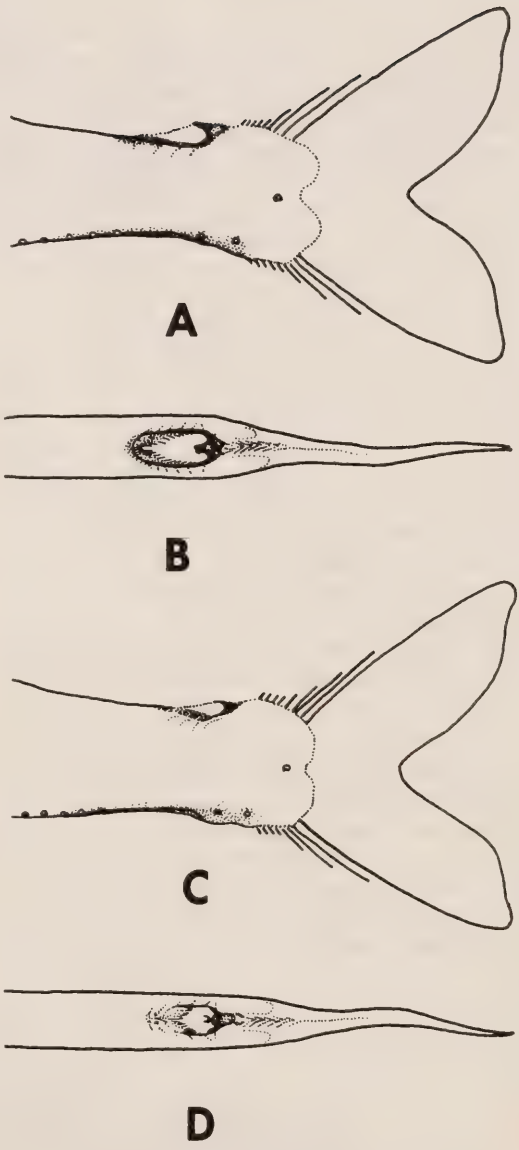

FIGURE 2.—*Taaningichthys minimus*. A. Side view, sexually dimorphic supracaudal gland of male, 53 mm. B. Top view, sexually dimorphic supracaudal gland of same male. C. Side view, sexually dimorphic supracaudal gland of female, 54 mm. D. Top view, sexually dimorphic supracaudal gland of same female.

diameters below horizontal septum. Prc_1 and Prc_2 level, behind infracaudal gland; Prc_3 at horizontal septum.

Caudal luminous glands undivided, the infracaudal larger than the supracaudal and both covered by scales. Sexual dimorphism is evident in supracaudal gland of adults (specimens about 40 mm and larger); in males this gland is about twice as large as in females (Figure 2).

Mesopterygoid teeth in narrow oval patches. Narrow band of needlelike teeth on palatine. No vomerine teeth. Both jaws with needlelike teeth which bend medially. A single row of broad-based, anteriorly hooked teeth occupying posterior two-thirds of medial surface of dentary. As many as five pairs of similar teeth, most often directed posteriorly, on medial surface of dentary near symphysis, and another two to three pairs projecting forward and laterally on symphysial area of premaxillary; below these, on anterior part of premaxillary, several posteriorly curved teeth (longer than rest of premaxillary teeth).

Taaningichthys minimus is the shallowest dwelling, most firm-bodied, and smallest of the three species, the largest examined specimen measuring 65 mm.

Gravid females (about 40 mm and larger) were captured in August-September.

Horizontal distribution—*T. minimus* occurs circumglobally between about lat 35° N and 30° S (Figure 5). It has been taken less frequently than *T. bathyphilus*.

Vertical distribution—Closing-net data from the Project "Ocean Acre" in the north Atlantic Ocean suggest vertical stratification of juveniles and adults. Juveniles appear to inhabit depths of 140 to 250 m, the smallest specimen (21 mm) having been captured at 140 m. Adults occur predominantly in depths between 450 and 500 m. *T. minimus* does not appear to perform daily vertical migrations.

Taaningichthys bathyphilus (Tåning, 1928)

Figure 3

Lampadena bathyphila Tåning, 1928: 63; Parr, 1928: 151, Figure 36.

Lampadena (*Lampadena*) *bathyphila* Fraser-Brunner, 1949: 1078, Figure.

Taaningichthys bathyphilus Bolin, 1959: 26, Figure 6.

D 12-13 (11-14); A 13 (12-14); P 12-14; V 8; gill rakers 3+1+7-8 (5-9), total 11-12 (9-13); VO 4 (3-5); AO 3 (1-4)+1(2), total 4(2-5); Prc 2+1; vertebrae 34-36; procurrent caudal rays 7+6.

Mouth terminal, moderately large, JL about 1.5 in Pre P; maxillary slightly expanded posteriorly. Eye large, ED about 2.5 in Pre P. Pterotic spine inconspicuous. Opercular margin as in *T. minimus*. Pectoral rays reaching VO_1; base of pectoral fin nearer to horizontal septum than to ventral margin of body. Pre V 2.1-2.5 in SL. Pre D 1.9-2.2 in SL; end of base of dorsal fin on, or slightly in advance of, vertical through SAO. Pre A 1.5-1.7 in SL. Base of adipose fin above end of base of anal fin; Pre Ad 1.2-1.4 in SL.

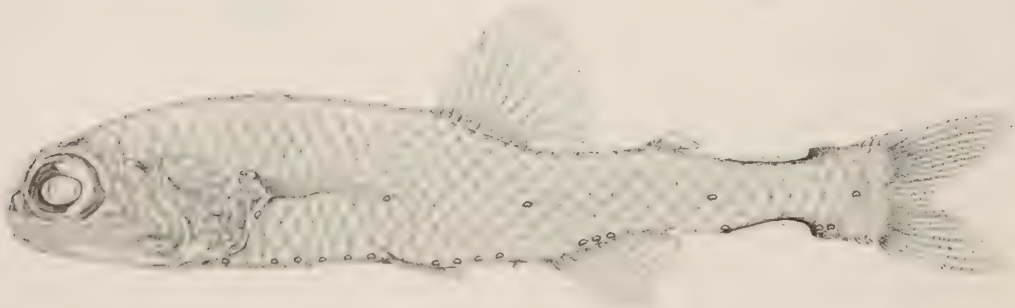

FIGURE 3.—*Taaningichthys bathyphilus* (Tåning); 62 mm, RV *Velero* stn. 11733, LACM 30034-1.

FIGURE 4.—*Taaningichthys paurolychnus*, new species, holotype, 67 mm, SIO 70-19.

Dn absent; a very small oval Vn, visible in young individuals and masked by darkly pigmented tissue in adults. Position of PVO_1 farther forward than in *T. minimus*, a line through PVO_1 and PVO_2 passing behind PLO; PVO_1 midway between upper end of base of pectoral fin and ventral margin of body; PVO_2 midway between PVO_1 and upper end of base of pectoral fin. PLO varying in position, usually closer to horizontal septum than upper end of base of pectoral fin. PO 5-6. VLO above base of pelvic fins, closer to horizontal septum than ventral margin of body. VO level. SAO 1-2 photophore diameters below horizontal septum, directly above or slightly behind urogenital papilla. AO level; AOp over anterior end of infracaudal gland. Pol position variable, generally midway between anterior end of infracaudal gland and end of base of anal fin (always well behind base of adipose fin), and one photophore diameter or less below horizontal septum. Prc_1 and Prc_2 level; Prc_3 at horizontal septum. Secondary photophores present on snout and rays of caudal fin.

Length of supracaudal luminous gland 1.5-2 in length of infracaudal; sexual dimorphism not apparent; both glands undivided and surrounded by dark pigment.

Mesopterygoid teeth rather sparsely distributed. Single row of needlelike teeth on palatines. No vomerine teeth. Both jaws with needlelike teeth which bend medially (those on the anteriormost premaxillary somewhat longer). Several broad-based, anteriorly hooked teeth on posterior medial surface of dentary (not as many as in *T. minimus*). Two to three pairs of similar teeth projecting forward and laterally on symphysial area of premaxillary.

Taaningichthys bathyphilus is the intermediate of the three species in terms of depth of occurrence, photophore development and size. It does not seem to grow larger than about 80 mm.

Of the specimens examined, only one gravid female (57 mm) was found which had been captured in late June.

Horizontal distribution—*T. bathyphilus* occurs circumglobally within a broad zone between lat 41° N and 67°31′ S (Figure 5). It appears to be more common or, perhaps, more easily captured than its two congeners.

Vertical distribution—The shallowest depth of capture for *T. bathyphilus* is 580 m (a juvenile male, 32 mm). An adult female, 65-mm long, was captured at a depth of 675 m. Members of this species have not been taken above these depths. The maximum depth of occurrence is not yet known. *T. bathyphilus* does not appear to perform daily vertical migrations.

Taaningichthys paurolychnus, NEW SPECIES

Figure 4

Holotype: 1 (67 mm), 17 Dec. 1969, 31° N, 119° W, Scripps Institution of Oceanography.

Paratypes: 1 (68 mm), 22 Nov. 1969, 17° 47′ N, 25°22′ W, National Institute of Oceanography; 1 (87 mm), 13 Sept. 1968, 17° S,

86° W, Institute of Oceanology, Academy of Sciences of the USSR, Moscow; 1 (49 mm), 20 Sept. 1961, 33° N, 17° W, Museu Municipal do Funchal; 1 (57 mm), 29 Jan. 1922, 19° N, 79° W, Zoological Museum, University of Copenhagen; 2 (79-95 mm), 17 Dec. 1969, 31° N, 119° W, 2 (65-71 mm), 10 June 1967, 35° N, 123° W, Scripps Institution of Oceanography; 1 (75 mm), 17 Sept. 1966, 1° N, 81° W, 1 (80 mm), 15 Jan. 1969, 32° N, 120° W, Smithsonian Oceanographic Sorting Center; 1 (82 mm), 13 Apr. 1962, 30° N, 120° W, 1 (77 mm), 29 Mar. 1962, 35° N, 129° W, National Marine Fisheries Service.

D 12-13 (11); A 13 (11-14); P 14 (13-15); V 8; gill rakers 3-4+1+9-10 (8-11), total 13-15 (12-16); vertebrae 35-36; procurrent caudal rays 7+6-7.

Mouth terminal, moderately large, JL about 1.5 in Pre P. Eye large, ED 2.2-3.2 in Pre P. A short pterotic spine directed posterolaterally. Opercular margin slightly concave posterodorsally to a level above upper end of base of pectoral fin, slightly convex posteriorly. Pectoral rays reaching base of pelvic fins; base of pectoral fin midway between ventral margin of body and horizontal septum. Pre V 2.1-2.3 in SL. Pre D 1.9-2.1 in SL; end of base of dorsal fin in advance of origin of anal fin. Pre A 1.5-1.7 in SL. Base of adipose fin directly above, or somewhat behind end of base of anal fin; Pre Ad 1.2-1.4 in SL.

Vn apparently absent. Head and body photophores absent. Secondary photophores present on snout and interradial membranes of caudal fin.

Length of supracaudal luminous gland 1.5-2 in length of infracaudal gland; sexual dimorphism not apparent; both glands undivided and surrounded by dark pigment.

Mesopterygoid teeth rather sparsely distributed. Single row of needlelike teeth on palatine. No vomerine teeth. Both jaws with needlelike teeth which bend medially (those on the anterior part of premaxillary somewhat longer). Several broad-based, anteriorly hooked teeth on posterior medial surface of dentary as in *T. bathyphilus*. Two to three pairs of similar teeth projecting forward and laterally on symphysial area of premaxillary.

Taaningichthys paurolychnus is the largest of the three species, the longest specimen examined measuring 95 mm. It has apparently lost its

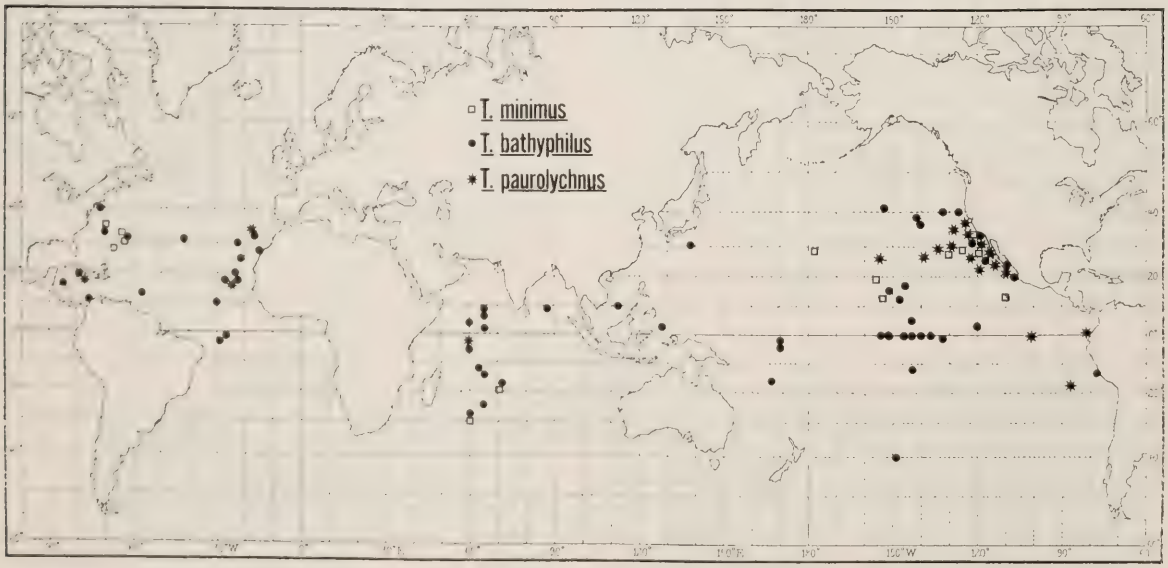

FIGURE 5.—Catch localities of *Taaningichthys minimus*, *T. bathyphilus*, and *T. paurolychnus*. Capture locality for specimen taken from 67°31′ S/90°26′ W not shown.

primary photophores, retaining only the caudal glands and the simple, presumably secondary, photophores, on the head and caudal fin. It is also the deepest dwelling of the three species.

Gravid females have been captured in March-April and August-September. The smallest gravid female examined was 65 mm.

Horizontal distribution—*T. paurolychnus* is distributed circumglobally between about lat 40° N and 20° S (Figure 5). It does not appear to be as common as *T. bathyphilus*.

Vertical distribution—*T. paurolychnus* has not been taken above 900 m (an adult female, 77 mm). The lower limits of its distribution are not yet known. *T. paurolychnus* does not appear to perform daily vertical migrations.

Etymology—The name *paurolychnus* refers to the absence of primary photophores and the presence of limited, presumably secondary photophores. It is derived from the Greek *pauros* meaning few, small, and *lychnus* meaning light.

OTOLITHS

OL as a percentage of SL ranges from 4.4 to 5.5% in *T. minimus*, 3.9 to 4.6% in *T. bathyphilus*, and 2.8 to 3.6% in *T. paurolychnus*. OH as a percentage of OL ranges from 66.7 to 77.7% in *T. minimus*, 72.1 to 77.9% in *T. bathyphilus*, and 78.3 to 91.7% in *T. paurolychnus*.

The sulcus is more pronounced in the otolith of *T. bathyphilus* than it is that of *T. paurolychnus*, but less so than in that of *T. minimus* (Figure 6). The otolith of *T. paurolychnus* has almost no antirostrum, and the antirostrum in *T. bathyphilus* is less pronounced than that in *T. minimus*. The posterior margin of the otolith in *T. paurolychnus* is nearly straight vertically, making the general outline almost square, whereas the otoliths of its two congeners are smoothly rounded posteroventrally, so that the general outline is oval. The otolith (Figure 6) of a single specimen of *T. bathyphilus* from the north Atlantic is differently shaped and very large for a specimen of its size (60 mm). However, no other differences in the fish were found and more material from the north Atlantic must be examined before anything further can be stated.

DISCUSSION

The various hypotheses and ideas regarding the function, or functions, of luminous organs of midwater fish are reviewed by Nicol (1969). The photophores within the genus *Taaningichthys* show drastic reduction in terms of numbers and development. *T. minimus* has, relatively, the best developed photophores as well as the greatest number; these organs are seldom rubbed off unless the specimen is damaged. *T. bathyphilus* has fewer and less well-developed photophores which are easily rubbed off. *T. paurolychnus* has lost all primary photophores but retains simple, presumably secondary, photophores on the snout and caudal fin. As already mentioned, there are no indications that the members of the genus *Taaningichthys* undertake diel vertical migrations as most myctophids do. It may therefore be that photophores of the myctophid type are not selected for in a deep-water, nonmigratory fish, which would account for the reduction of these organs and, eventually, their loss. Unlike photophores, eyes are very well developed in *Taaningichthys*, regardless of depth of occurrence. Even the deepest of the species has large, nearly binocular eyes. This may be correlated with the food habits of these fish. Myctophids, in general, feed on zooplankters, many, if not most, of which are bioluminescent. It is possible therefore that *Taaningichthys* strongly depends on large, presumably highly effective eyes for locating and capturing its prey, which is probably not very abundant in those dark midwater depths. Furthermore, retention of this energetically expensive visual equipment may account for the very poorly developed lateral line system.

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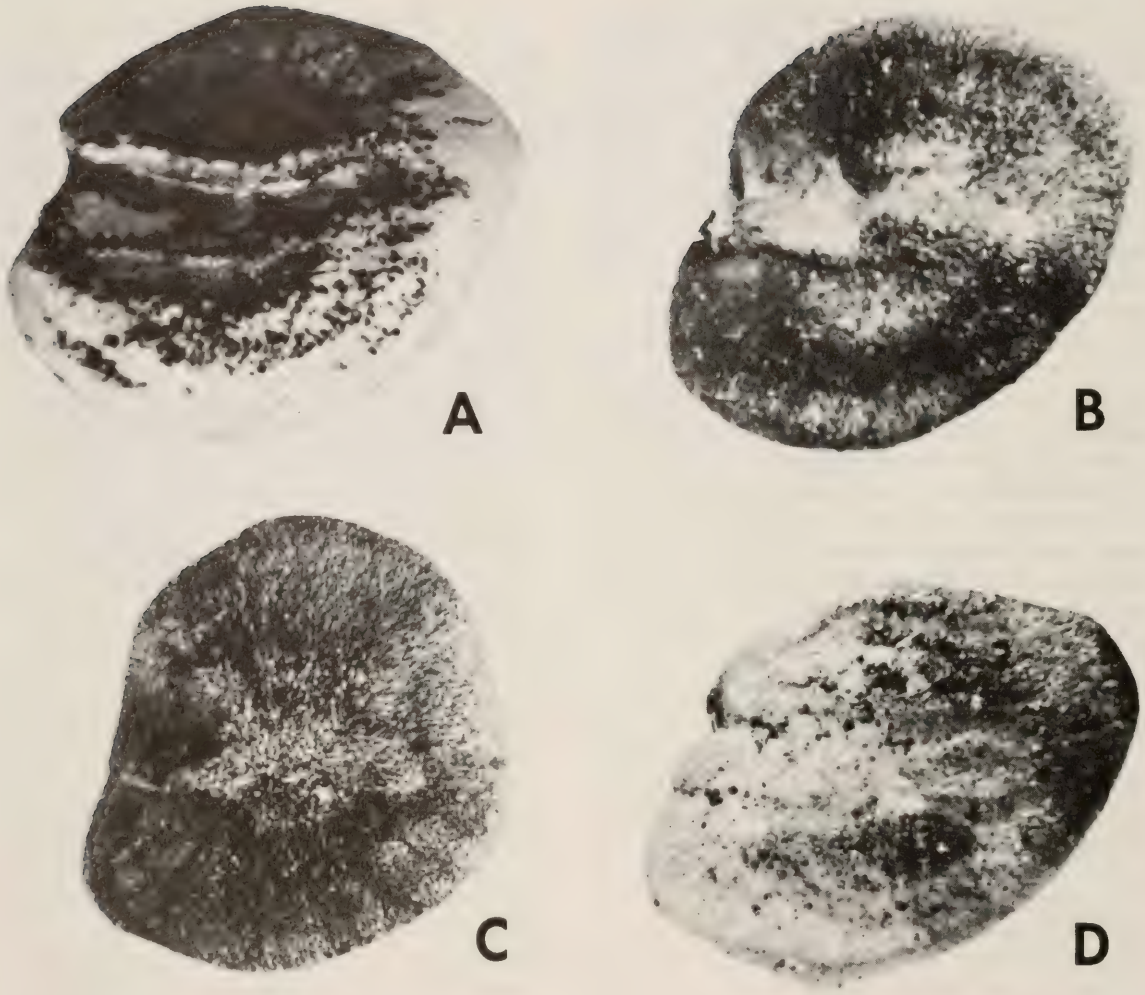

FIGURE 6.—Medial views of right otoliths, anterior end to the left.
A. *Taaningichthys minimus*, otolith 2.0 mm long, specimen 49 mm.
B. *T. bathyphilus*, otolith 1.8 mm long, specimen 64 mm.
C. *T. paurolychnus*, otolith 1.7 mm long, specimen 87 mm.
D. *T. bathyphilus*, otolith 2.3 mm long, specimen (from north Atlantic) 60 mm.

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I am grateful to my friend Lu Duffy for having typed the manuscript.

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APPENDIX

Material examined

Taaningichthys minimus

University of Southern California, RV *Velero IV*:
Stn. 11168, 31 July 1966, 32° N/120° W, 350 m, 10-ft IKMT, 1 (36 mm), LACM 9705.
Stn. 11185, 2 Aug. 1966, 29° N/118° W, 375 m, 10-ft IKMT, 1 (47 mm), LACM 9650.

International Indian Ocean Expedition, RV *Anton Bruun*, Cruise III:
Stn. 156, 6 Sept. 1963, 29° S/60° E, 122 m, 10-ft IKMT, 1 (45 mm), LACM 31320.

University of Hawaii, Institute of Marine Biology:
LACM 31574, 11 Sept. 1969, Hawaiian waters, 380 m, 6-ft IKMT, 2 (55-57 mm).
LACM 31575, 30 Oct. 1969, Hawaiian waters, 780 m, 6-ft IKMT, 2 (63-65 mm).
LACM 31576, 13 Nov. 1969, Hawaiian waters, 575 m, 10-ft IKMT, 2 (50-60 mm).

Scripps Institution of Oceanography:
SIO 57-86, 12 May 1955, 29° N/125° W, 700 m, 10-ft IKMT, 1 (42 mm).
SIO 62-430, 24 Aug. 1962, 29° N/130° W, 600 m, 10-ft IKMT, 1 (52 mm).
SIO 68-490, 22 Sept. 1968, 29° N/178° W, no depth, 10-ft IKMT, 1 (46 mm).
SIO 69-341, 27 Mar. 1969, 13° N/110° W, 1,100 m, 10-ft IKMT, 1 (42 mm).

Woods Hole Oceanographic Institution:
RHB stn. 1112, 17 June 1965, 22° N/70° W, 200 m, 10-ft IKMT, 1 (28 mm).
RHB stn. 1735, 8 July 1968, 28° N/67° W, 870 m, 10-ft IKMT, 1 (40 mm).

Zoological Institute, Academy of Sciences of the USSR, Leningrad:
RV *Vitiaz* stn. 4885, 20 Dec. 1960, 17° S/71° E, 2,700 m, RT, 1 (27 mm).
RV *Vitiaz* stn. 5127, 28 Oct. 1961, 13° N/154° W, 1,000 m, CN, 1 (48 mm).

National Marine Fisheries Service, RV *Horizon*:
Cruise H6204, stn. 100-140, 15 Apr. 1962, 28° N/124° W, 1,676 m, 10-ft IKMT, 1 (53.5 mm).
Cruise H6204, stn. 110-160, 17 Apr. 1962, 35° N/124° W, 1,676 m, 10-ft IKMT, 1 (50 mm).

U.S. National Museum, Ocean Acre material:
Stn. 2-2N, 6 Mar. 1967, 32°26′ N/63°44′ W, 140 m, 6-ft IKMT, 1 (21 mm).
Stn. 3-3N, 4 July 1967, 33°4′ N/64°37′ W, 1,060 m, 10-ft IKMT, 1 (52.5 mm).
Stn. 3-4N, 4 July 1967, 33°10′ N/64°45′ W, 480 m, 10-ft IKMT, 1 (37 mm).
Stn. 3-6N, 5 July 1967, 33°9′ N/64°33′W, 250 m, 10-ft IKMT, 3 (36-45.2 mm).
Stn. 3-13N, 6 July 1967, 32°54′ N/64°45′ W, 161 m, 10-ft IKMT, 1 (20.5 mm).
Stn. 4-9A, 4 Sept. 1967, 31°52′ N/63°58′ W, 479 m, 10-ft IKMT, 1 (49 mm).
Stn. 4-9B, 4 Sept. 1967, 31°52′ N/63°58′ W, 479 m, 10-ft IKMT, 1 (42 mm).
Stn. 4-16C, 6 Sept. 1967, 32° N/64° 17′ W, 500 m, 10-ft IKMT, 1 (41 mm).
Stn. 6-7B, 26 Apr. 1967, 31°47′ N/63°53′ W, 155 m, 10-ft IKMT, 1 (33.5 mm).

Stn. 6-15B, 28 Apr. 1967, 32°13′ N/63°51′ W, 160 m, 10-ft IKMT, 1 (33 mm).
Stn. 6-15P, 28 Apr. 1967, 32°13′ N/63°51′ W, 160 m, 10-ft IKMT, 1 (34.5 mm).
Stn. 6-18P, 29 Apr. 1967, 32°14′ N/63°46′ W, 750 m, 10-ft IKMT, 1 (30 mm).
Stn. 6-26N, 30 Apr. 1967, 32°18′ N/63°55′ W, 200 m, 10-ft IKMT, 1 (29 mm).
Stn. 7-14N, 8 Sept. 1967, 32°12′ N/63°25′ W, 250 m, 10-ft IKMT, 1 (45 mm).
Stn. 7-15N, 8 Sept. 1967, 32°21′ N/63°29′ W, 450 m, 10-ft IKMT, 1 (42 mm).

Taaningichthys bathyphilus

University of Southern California, RV *Eltanin*:
Stn. 947, 27 Jan. 1964, 67°31′ S/90°26′ W, 2,690 m, 3-m IKMT, 1 (67 mm), LACM 10424.
Stn. 1724, 18 July 1966, 40°06′ S/149°55′ W, 1,180 m, 3-m IKMT, 1 (60 mm), LACM 11247.

University of Southern California, RV *Velero IV*:
Stn. 8959, 17 Oct. 1963, 33° N/119° W, 900 m, 10-ft IKMT, 1 (69 mm), LACM 6435.
Stn. 10607, 10 June 1965, 33° N/119° W, 900 m, 10-ft IKMT, 1 (61 mm), LACM 6723.
Stn. 966, 15 May 1964, 33° N/118° W, 750 m, 10-ft IKMT, 1 (72 mm), LACM 8525.
Stn. 8238, 25 Oct. 1962, 33° N/118° W, 10-ft IKMT, 1 (64 mm), LACM 9036.
Stn. 9860, 25 June 1964, 33° N/118° W, 750 m, 10-ft IKMT, 1 (60 mm), LACM 9089.
Stn. 11538, 21 June 1967, 32° N/118° W, 1,300 m, 10-ft IKMT, 1 (66 mm), LACM 9676.
Stn. 11539, 21 June 1967, 33° N/118° W, 950 m, 10-ft IKMT, 1 (63 mm), LACM 9677.
Stn. 11617, 16 Aug. 1967, 31° N/118° W, 1,130 m, 10-ft IKMT, 1 (68 mm), LACM 9682.
Stn. 11312, 25 Jan. 1967, 28° N/116° W, 1,325 m, 10-ft IKMT, 1 (58 mm), LACM 9708.
Stn. 10373, 23 Feb. 1965, 33° N/118° W, 10-ft IKMT, 2 (61-68 mm), LACM 9764.
Stn. 11696, 12 Oct. 1967, 32° N/118° W, 860 m, 10-ft IKMT, 1 (67 mm), LACM 9796.
Stn. 11733, 8 Nov. 1967, 20° N/106° W, 1,400 m, 10-ft IKMT, 1 (62 mm), LACM 30034.
Stn. 11767, 16 Nov. 1967, 24° N/109° W, 1,500 m, 10-ft IKMT, 1 (57 mm), LACM 30045.
Stn. 12066, 12 Apr. 1968, 26° N/114° W, 1,300 m, 10-ft IKMT, 1 (61 mm), LACM 30075.
Stn. 12072, 14 Apr. 1968, 29° N/118° W, 750 m, 10-ft IKMT, 1 (65 mm), LACM 30079.
Stn. 12184, 24 July 1968, 31° N/119° W, 820 m, 10-ft IKMT, 1 (50 mm), LACM 30271.
Stn. 12597, 17 Jan. 1969, 32° N/120° W, 770 m, 10-ft IKMT, 1 (67 mm), LACM 30348.
Stn. 12392, 11 Oct. 1968, 32° N/118° W, 1,110 m, 10-ft IKMT, 1 (61 mm), LACM 30403.
Stn. 12349, 12 Sept. 1968, 32° N/118° W, 1,400 m, 10-ft IKMT, 1 (67 mm), LACM 20598.
Stn. 12491, 20 Nov. 1968, 29° N/118° W, 910 m, 10-ft IKMT, 2 (61-65 mm), LACM 30609.
Stn. 13385, 28 Oct. 1969, 28° N/118° W, 780 m, 10-ft IKMT, 1 (68 mm), LACM 30886.

Smithsonian Oceanographic Sorting Center, RV *Anton Bruun*, Cruise III and VI:
Label no. 7033, 18 Aug. 1963, 4° N/60° E, 2,120 m, 10-ft IKMT, 1 (34 mm), LACM 31292.
Label no. 7057, 23 Aug. 1963, 5° S/60° E, 2,030 m, 10-ft IKMT, 1 (26 mm), LACM 31303.
Label no. 7083, 6 Sept. 1963, 29° S/60° E, 1,150 m, 10-ft IKMT, 7 (44-55 mm), LACM 31320.
Label no. 7173, 23 May 1964, 8° N/65° E, 2,850 m, 10-ft IKMT, 1 (44 mm), LACM 31344.
Label no. 7177, 23 May 1964, 7° N/65° E, 940 m, 10-ft IKMT, 1 (36 mm), LACM 31345.
Label no. 7204, 27 May 1964, 2° N/65° E, 1,250 m, 10-ft IKMT, 1 (46 mm), LACM 31358.
Label no. 7217, 28 May 1964, 14° S/65° E, 2,250 m, 10-ft IKMT, 1 (53 mm), LACM 31361.
Label no. 7265, 4 June 1964, 12° S/64° E, 1,930 m, 10-ft IKMT, 1 (38 mm), LACM 31375.
Label no. 7273, 6 May 1964, 14° S/65° E, 880 m, 10-ft IKMT, 1 (47 mm), LACM 31376.
Label no. 7305, 24 June 1964, 24° S/65° E, 3,500 m, 10-ft IKMT, 1 (57 mm), LACM 31401.
Label no. 7312, 25 June 1964, 24° S/65° E, 1,100 m, 10-ft IKMT, 1 (56 mm), LACM 31404.

Office de la Recherche Scientifique et Technique Outre-Mer, Nouméa, New Caledonia:
RV *Caride*, Cruise I, stn. 36A, 23 Sept. 1968, 0°2′ N/137°51′ W, 950 m, 10-ft IKMT, 3 (51-60 mm), LACM 31439.
RV *Caride*, Cruise I, stn. 39A, 24 Sept. 1968, 0°14′ N/138°17′ W, 1,130 m, 10-ft IKMT, 1 (46 mm), LACM 31440.
RV *Caride*, Cruise I, stn. 69A, 29 Sept. 1968, 0°5′ N/144°41′ W, 580 m, 10-ft IKMT, 1 (32 mm), LACM 31446.
RV *Caride*, Cruise I, stn. 74A, 29 Sept. 1968, 0°/145°41′ W, 820 m, 10-ft IKMT, 1 (58 mm), LACM 31448.
RV *Caride*, Cruise I, stn. 77A, 30 Sept. 1968, 0°25′ N/146°17′ W, 1,110 m, 10-ft IKMT, 1 (48 mm), LACM 31450.
RV *Caride*, Cruise I, stn. 78A, 30 Sept. 1968, 0°2′ S/146°29′ W, 1,280 m, 10-ft IKMT, 1 (42 mm), LACM 31451.
RV *Caride*, Cruise III, stn. 17, 7 Feb. 1969, 11°17′ S/142°47′ W, 1,050 m, 10-ft IKMT, 1 (60 mm), LACM 31459.
RV *Caride*, Cruise III, stn. 18, 8 Feb. 1969, 11°7′ S/142°35′ W, 1,050 m, 10-ft IKMT, 1 (53 mm), LACM 31460.
RV *Caride*, Cruise III, stn. 60, 18 Feb. 1968, 0°12′ S/139°19′ W, 850 m, 10-ft IKMT, 1 (55 mm), LACM 31464.
RV *Caride*, Cruise III, stn. 64, 19 Feb. 1969, 0°/140°9′ W, 900 m, 10-ft IKMT, 1 (48 mm), LACM 31467.
RC *Caride*, Cruise III, stn. 68, 10 Feb. 1969, 0°/140°42′ W, 1,080 m, 10-ft IKMT, 1 (29 mm), LACM 31469.
RV *Caride*, Cruise III, stn. 122, 24 Feb. 1970, 0°3′N/147°2′ W, 1,100 m, 10-ft IKMT, 2 (45-51 mm), LACM 31478.
RV *Caride*, Cruise III, stn. 200, 2 March 1970, 0°1′ N/154°14′ W, 930 m, 10-ft IKMT, 1 (46 mm), LACM 31491.
RV *Caride*, Cruise III, stn. 204, 2 March 1970, 0°/154°25′ W, 1,160 m, 10-ft IKMT, 1 (34 mm), LACM 31492.
RV *Cyclone*, Cruise III, stn. 8, 4 May 1967, 2°13′ S/169°47′ E, 1,125 m, 10-ft IKMT, 1 (37 mm), LACM 31501.
RV *Cyclone*, Cruise III, stn. 17, 5 May 1967, 4°23′ S/169°52′ E, 1,090 m, 10-ft IKMT, 1 (51 mm), LACM 31505.
RV *Santo*, Cruise 68, stn. 6, 20 July 1968, 16°17′ S/166°40′ E, 1,395 m, 10-ft IKMT, 1 (52 mm), LACM 31528.

U.S. National Museum: Ocean Acre material:
Stn. 3-2N, 4 July 1967, 33° N/64°45′ W, 1,425 m, 10-ft IKMT, 1 (44 mm).
Stn. 3-11N, 5 July 1967, 33° N/64°40′ W, 1,920 m, 10-ft IKMT, 2 (53-58 mm).
Stn. 6-10B, 27 Apr. 1967, 31°59′ N/63°43′ W, 900 m, 10-ft IKMT, 1 (55 mm).
Stn. 6-24N, 30 Apr. 1967, 32°13′ N, 63°40′ W, 750 m, 10-ft IKMT, 1 (67 mm).
Stn. 7-13N, 8 Sept. 1967, 32°18′ N/63°30′ W, 1,500 m, 10-ft IKMT, 1 (36 mm).

Carlsberg Foundation, *Dana* collections:
Dana stn. 1156 VII, 25 Oct. 1921, 25° N/21° W, 2,000 m, S 150, 1 (37 mm).
Dana stn. 1159 II, 29 Oct. 1921, 18° N/24° W, 2,000 m, S 150, 1 (43 mm).
Dana stn. 1159 III, 29 Oct. 1921, 18° N/24° W, 1,500 m, S 150, 1 (35 mm).
Dana stn. 1181 III, 21 Nov. 1921, 13° N/57° W, 1,500 m, S 150, 1 (28 mm).
Dana stn. 1217 III, 29 Jan. 1922, 19° N/79° W, 1,500 m, S 150, 1 (45 mm).
Dana stn. 1342 I, 15 May 1922, 34° N/70° W, 2,250 m, E 300, 1 (43 mm).
Dana stn. 1365 IX, 8 June 1922, 32° N/42° W, 2,500 m, E 300, 1 (55 mm).

Zoological Institute, Academy of Sciences of the USSR, Leningrad:
RV *Lyra* stn. 50, 25 Mar. 1966, 3° N/120° W, 1,000 m, CN, 1 (43 mm).
RV *Lyra* stn. 3717, 9 Jan. 1957, 3° N/128° E, 1,250 m, CN, 1 (35 mm).
RV *Vitiaz* stn. 4183, 6 Dec. 1958, 40° N/127° W, 675 m, CN, 1 (65 mm).
RV *Vitiaz* stn. 4189, 7 Dec. 1958, 40° N/133° W, 1,000 m, CN, 1 (49 mm).
RV *Vitiaz* stn. 4939, 4 Feb. 1961, 9° N/87° E, 1,000 m, CN, 1 (39 mm).

National Institute of Oceanography, Surrey, England:
NIO stn. 4687, 30 Aug. 1961, 29°57′ N/32°3′ W, 800 m, IKMT, 1 (50 mm).
NIO stn. 4746, 30 Sept. 1961, 29°59′ N/22°56′ W, 1,100 m, IKMT, 2 (38-44 mm).
NIO stn. 5799, 19 Oct. 1965, 28°9′ N/14°9′ W, 675 m, IKMT, 1 (48 mm).
NIO stn. 5810, 7 Nov. 1965, 28°4′ N/13°51′ W, 800 m, IKMT, 1 (28 mm).
NIO stn. 5813, 10 Nov. 1965, 28°5′ N/14°11′ W, 950 m, IKMT, 1 (56 mm).
NIO stn. 6687, 7 Mar. 1968, 20°37′ N/22°56′ W, 1,000 m, RMT8, 1 (56 mm).
NIO stn. 7072, 30 Oct. 1969, 20°27′ N/25°32′ W, 1,000 m, RMT8, 2 (32-55 mm).
NIO stn. 7079, 3 Nov. 1969, 17°40′ N/27°6′ W, 1,000 m, RMT8, 1 (24 mm).
NIO stn. 7089 #54, 22 Nov. 1969, 17°47′ N/25°22′ W, 1,000 m, RMT8, 2 (54-77 mm).
NIO stn. 7089 #55, 22 Nov. 1969, 17°47′N/25°22′ W, 2,000 m, RMT8, 1 (46 mm).

British Museum of Natural History:
Rosaura collection, 26 June 1969, 17° N/86° W, 1,100 m, S 200, 1 (57 mm).
Rosaura collection, 26 June 1969, 11° N/76° W, 1,200 m, S 200, 1 (46 mm).

National Marine Fisheries Service, RV *Horizon*:
Cruise H6204 stn. 120-70, 23 Apr. 1962, 26° N/117° W, 1,676 m, 10-ft IKMT, 1 (65 mm).

Woods Hole Oceanographic Institution:
RHB stn. 977, 26 Feb. 1963, 1° S/27° W, 10-ft IKMT, 1,100 m, 1 (65 mm).
RHB stn. 979, 28 Feb. 1963, 3° S/29° W, 10-ft IKMT, 1,100 m, 1 (57 mm).
RHB stn. 1603, 6 Oct. 1967, 39°46′ N/70°30′ W, 10-ft IKMT, 1,000 m, 1 (65 mm).

Taaningichthys paurolychnus

University of Southern California, RV *Velero IV*:
Stn. 10675, 28 Aug. 1965, 29° N/118° W, 1,625 m, 10-ft IKMT, 1 (44 mm), LACM 9350.
Stn. 11187, 2 Aug. 1966, 29° N/118° W, 1,720 m, 10-ft IKMT, 1 (87 mm), LACM 9567.
Stn. 11257, 21 Oct. 1966, 29° N/118° W, 940 m, 10-ft IKMT, 1 (77 mm), LACM 9408.
Stn. 11628, 18 Aug. 1967, 32° N/119° W, 1,300 m, 10-ft IKMT, 1 (33 mm), LACM 9693.
Stn. 12331, 24 Aug. 1968, 29° N/118° W, 1,100 m, 10-ft IKMT, 1 (55 mm), LACM 30284.
Stn. 12340, 26 Aug. 1968, 32° N/118° W, 1,130 m, 10-ft IKMT, 1 (17 mm), LACM 30591.
Stn. 12475, 18 Nov. 1968, 28° N/119° W, 900 m, 10-ft IKMT, 1 (42 mm), LACM 30606.
Stn. 12483, 19 Nov. 1968, 28° N/119° W, 2,080 m, 10-ft IKMT, 3 (52-81 mm), LACM 30382.
Stn. 12592, 15 Jan. 1969, 32° N/120° W, 1,950 m, 10-ft IKMT, 3 (23-82 mm), LACM 30429.
Stn. 12593, 16 Jan. 1969, 32° N/120° W, 1,920 m, 10-ft IKMT, 1 (91 mm), LACM 30430.
Stn. 12594, 16 Jan. 1969, 32° N/120° W, 1,250 m, 10-ft IKMT, 1 (79 mm), LACM 30431.
Stn. 12786, 16 Mar. 1969, 32° N/118° W, 1,350 m, 10-ft IKMT, 1 (66 mm), LACM 30423.
Stn. 12791, 17 Mar. 1969, 32° N/118° W, 1,200 m, 10-ft IKMT, 1 (64 mm), LACM 30428.

Smithsonian Oceanographic Sorting Center, RV *Anton Bruun*, Cruise III and VI:
Label no. 7057, 23 Aug. 1963, 4° S/60° E, 2,030 m, 10-ft IKMT, 1 (51 mm), LACM 31303.

National Marine Fisheries Service, RV *Horizon*:
Cruise H6204 stn. 60.60, 26 Mar. 1962, 37° N/123° W, 1,863 m, IKMT, 1 (86 mm).
Cruise H6204 stn. 60.140, 29 Mar. 1962, 35° N/129° W, 1,863 m, IKMT, 1 (77 mm).
Cruise H6204 stn. 80.90, 18 Mar. 1962, 33° N/123° W, 2,234 m, IKMT, 1 (29 mm).
Cruise H6204 stn. 100.60, 13 Apr. 1962, 31° N/119° W, 1,676 m, IKMT, 1 (68 mm).
Cruise H6204 stn. 100.80, 13 Apr. 1962, 30° N/120° W, 1,676 m, IKMT, 1 (82 mm).

Scripps Institution of Oceanography:
SIO 54-95, 23 June 1954, 23° N/119° W, 2,500 m, 10-ft IKMT, 1 (49 mm).
SIO 60-283, 12 Aug. 1960, 28° N/135° W, 3,000 m, 10-ft IKMT, 1 (44 mm).
SIO 60-284, 13 Aug. 1960, 29° N/132° W, 3,000 m, 10-ft IKMT, 1 (71 mm).
SIO 64-11, 30 Jan. 1964, 24° N/113° W, 5,300 m, 10-ft IKMT, 1 (78 mm).
SIO 66-31, 5 Apr. 1966, 29° N/117° W, 4,000 m, 10-ft IKMT, 1 (84 mm).
SIO 67-52, 22 Apr. 1967, 30° N/117° W, 4,000 m, 10-ft IKMT, 1 (80 mm).

SIO 67-102, 10 June 1967, 35° N/123° W, 2,200 m, 10-ft IKMT, 2 (65-71 mm).
SIO 70-19, 17 Dec. 1969, 31° N/119° W, 4,000 m, 10-ft IKMT, 1 (67 mm).
SIO 70-20, 17 Dec. 1969, 31° N/119° W, 4,000 m, 10-ft IKMT, 2 (79-95 mm).

National Institute of Oceanography, Surrey, England:
NIO sta. 7089 #55, 22 Nov. 1969, 17°47′ N/25°22′ W, RMT8, 3 (45-73).

Zoological Institute, Academy of Sciences of the USSR, Leningrad:
RV *Akademik Kurchatov* stn. 233, 13 Sept. 1968, 17° S/86° W, 2,000 m, CN, 1 (87 mm), 39908.

Zoological Museum, University of Copenhagen:
Dana stn. 1217 I, 29 Jan. 1922, 19° N/79° W, 2,000 m, E 300, 1 (57 mm), P2330669.

Museu Municipal do Funchal, Madeira:
RV *Discovery* 4742, 20 Sept. 1961, 32°42′ N/16°32′ W, 1,700 m, IKMT, 1 (49 mm), MMF 22115.

SOME LIFE HISTORY CHARACTERISTICS OF COHO SALMON OF THE KARLUK RIVER SYSTEM, KODIAK ISLAND, ALASKA

BENSON DRUCKER[1]

ABSTRACT

This paper contains data on some life history characteristics of the coho salmon of the Karluk River system, Kodiak Island, Alaska: age, fecundity, length, and egg size of adults; and migration characteristics, age, and size of smolts. The greater age at maturity of Karluk coho salmon (4 and 5 years) because of the longer freshwater residence of the juveniles is unique among reported North American stocks and may result in greater freshwater mortality but less marine mortality because the smolts are larger when they enter the ocean. Fecundity of Karluk coho salmon also differs from that reported for other North American stocks in that they are extremely fecund—more similar to Asiatic stocks of the Kamchatka Peninsula.

Coho salmon, *Oncorhynchus kisutch*, are widely distributed along the Pacific coast of North America and occur in commercially harvestable quantities from northern California to northwestern Alaska. About one-third of the total North American commercial catch comes from Alaska waters, where from 1960 to 1968 the average annual catch of 16 million pounds was valued at almost $3.5 million to the fishermen.[2] The amount of biological research on coho salmon in Alaska is small, and published scientific reports on Alaska coho salmon stocks are very few.

In this paper I present data on some life history characteristics of the coho salmon of the Karluk River system. This system is located on the southwest side of Kodiak Island, Alaska, at approximately lat 57° N and long 154° W and includes Karluk Lake, tributaries to the lake, Thumb and O'Malley Lakes, and Karluk River (Figure 1). Information is presented on age, fecundity, length, and egg size of coho salmon adults; and migration characteristics, age, and

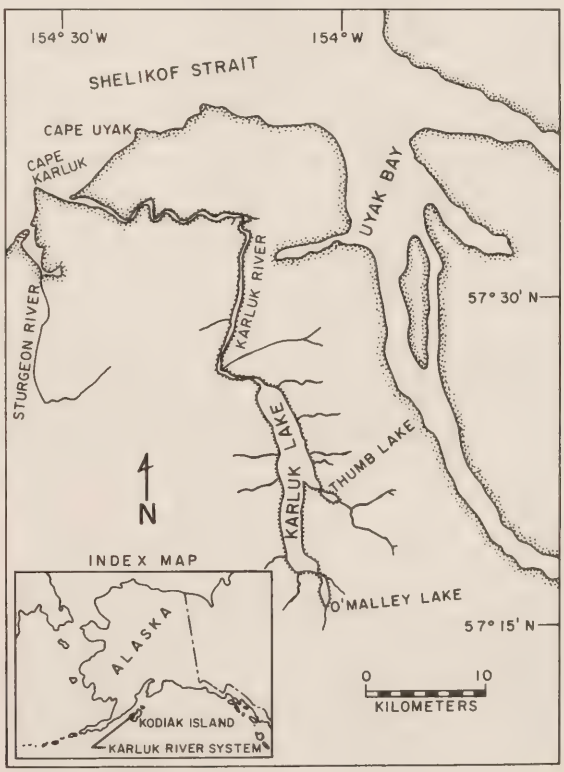

FIGURE 1.—The Karluk River system, Kodiak Island, Alaska.

[1] National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821; present address: National Marine Fisheries Service, Technical Advisory Division, Interior Building, Washington, D.C. 20235.

[2] Nelson, Richard C. 1968. Alaska catch and production, commercial fisheries statistics. Alaska Dep. Fish Game, Stat. Leafl. 17, 29 p. (Unpublished.)

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size of coho salmon smolts. These life history features of Karluk coho salmon are compared with those reported for various coho salmon stocks from other areas on both the Asiatic and North American sides of the Pacific Ocean. In addition, the effect of a prolonged juvenile freshwater residence, a feature unique to the Karluk system, on freshwater and marine survival is discussed. All of the data on Karluk coho salmon were collected incidentally during studies of sockeye salmon, *O. nerka*, the dominant salmon species in the Karluk system; much of the information on other Alaska stocks is from unpublished administrative and progress reports.

Because I intend to discuss differences between coho salmon in the Karluk system and those in other areas, a description of general features of the life cycle of coho salmon stocks is appropriate. Typically, the adults enter streams and rivers from late summer to November and spawn in late fall and early winter. Some Asiatic stocks, however, spawn as late as mid-March (Smirnov, 1960). The progeny emerge as fry in the spring following spawning and reside in rivers or lakes for 1 or 2 years before going to sea as smolts. In some areas the seaward smolt migration begins in late winter (Chapman, 1961; Smoker, 1953), but in most areas it takes place from April to August (Godfrey, 1965). The salmon grow rapidly in the ocean, and the adults return to the streams and rivers to spawn 12 to 18 months later. However, a significant percentage of male coho salmon, particularly in their southern range of distribution in North America (California), mature precociously (6 to 9 months after they enter salt water) and return to spawn the same year that they migrated to sea (Shapovalov and Taft, 1954). These fish are known as jack salmon.

METHODS

The data for adult coho salmon of the Karluk system were obtained from fish from the 1966 escapement that were captured at the adult counting weir or caught by sport fishermen at the outlet of Karluk Lake about 300 yards upstream from the weir site. All fish were measured for length (mideye to fork of tail) with a caliper to the nearest millimeter. Mideye-fork length was used because of morphological changes that occur as the fish matures, particularly the elongation of the snout. Ovaries for fecundity samples were removed from all females and were preserved in 10% Formalin solution for at least 48 hr. The eggs were then hand-counted to get total egg counts. The diameters of some eggs from the fecundity samples were measured. These eggs were removed directly from the ovary, water hardened, and placed in Stockard's solution. The diameters were then measured with a vernier measuring microscope calibrated to 0.01 mm. The ages of adult fish were determined by reading scales that had been taken halfway between the lateral line and the posterior insertion of the dorsal fin.

The data for smolts were obtained from fish captured in 1956, 1965, and 1968 in fyke nets fished on the downstream side of the adult counting weir. Fork lengths were taken to the nearest millimeter with a steel millimeter ruler, and weights were taken to the nearest tenth of a gram on a triple-beam balance. As with the adults, the ages of smolts were determined from scales taken halfway between the lateral line and the posterior insertion of the dorsal fin.

AGE OF COHO SALMON

The average age composition of coho salmon for several systems in northern and southern latitudes of North America and Asia is shown in Table 1. The differences from the northern to southern latitudes in age composition is similar to that noted by Marr (1943) and possibly represent a geographic cline.

The Karluk system had three freshwater age classes,[3] two of which were decidedly predominant (Table 1). The three age classes, 4_3, 5_4, and 6_5, designate fish that went to sea in their third, fourth, and fifth years of life and returned to spawn after being at sea for about 1 year.

[3] Age classes are designated according to the system developed by Gilbert and Rich (1927). A 4_3 coho salmon is in its fourth year of life. It went to sea as a smolt at the beginning of its third year, having spent two growing seasons in fresh water.

TABLE 1.—Age class composition of stocks of coho salmon from North America and Asia, arranged geographically from north to south.

Area	Percent coho salmon in age class—										Reference
	2_1	2_2	3_1	3_2	3_3	4_1	4_2	4_3	5_3	5_4	6_5	
North America												
Nome River, Alaska	--	--	--	29.4	--	--	--	70.6	--	--	--	Godfrey (1965)
Unalakleet River, Alaska	--	--	--	37.9	--	--	--	62.1	--	--	--	Godfrey (1965)
Yukon River, Alaska	--	--	--	55.6	--	--	--	44.4	--	--	--	Godfrey (1965)
Yukon River, Alaska	--	--	--	38.7	--	--	--	58.1	--	3.2	--	Gilbert (1922)
Cook Inlet River, Alaska	--	--	--	40.0	--	--	--	60.0	--	--	--	Godfrey (1965)
Resurrection Bay, Alaska	--	--	--	30.3	--	--	--	68.8	--	0.9	--	Logan (1963,[1] 1964[2])
Bear Creek, Alaska	--	--	--	27.1	--	--	--	71.1	--	1.8	--	Logan (1964)[2]
Dairy Creek, Alaska	--	--	--	[3]83.3	--	--	--	16.7	--	--	--	Logan (1964)[2]
Mendenhall River, Alaska	--	--	--	12.0	8.0	--	--	80.0	--	--	--	([4])
Hood Bay Creek, Alaska	--	--	--	46.5	--	--	--	47.5	--	6.0	--	Armstrong (1970)
Karluk River, Alaska	--	--	--	--	--	--	--	56.9	--	41.7	1.4	Present study
Sashin Creek, Alaska	--	--	--	18.0	--	--	--	77.0	--	5.0	--	Crone (1968)
Port Herbert, Alaska	--	--	--	20.0	--	--	--	76.0	--	4.0	--	Crone (1968)
Stikine River, Alaska	--	--	--	45.2	--	--	1.0	51.9	1.9	--	--	Godfrey (1965)
Chignik River, Alaska	--	--	--	23.2	--	--	--	72.4	--	4.4	--	Israel (1933)
Ketchikan River, Alaska	--	--	--	70.8	--	--	--	29.2	--	--	--	Godfrey (1965)
Quatsino Bay, British Columbia	--	2.0	--	95.0	--	--	3.0	--	--	--	--	Godfrey (1965)
Fraser River, British Columbia	2.6	--	0.7	96.5	--	--	0.2	--	--	--	--	Godfrey (1965)
Georgia Strait, British Columbia	1.5	0.6	0.4	97.1	--	--	0.4	--	--	--	--	Godfrey (1965)
West coast, Vancouver Island, British Columbia	1.3	--	0.6	97.5	--	--	0.4	0.2	--	--	--	Godfrey (1965)
Langara Island, Georgia Strait, British Columbia	0.1	0.1	0.2	97.9	Tr.	0.1	0.7	0.9	--	--	--	Pritchard (1940)
Columbia River, Wash.	--	6.1	--	83.9	0.3	--	--	9.7	--	--	--	Marr (1943)
Waddell Creek, Calif.	--	18.4	--	81.6	--	--	--	--	--	--	--	Shapovalov and Taft (1954)
Asia												
East coast of Kamchatka, USSR:												
Kamchatka River	--	1.2	--	55.7	--	--	--	43.1	--	--	--	Godfrey (1965); Gribanov (1948)
Lake Ushki	--	Tr.	--	4.3	Tr.	--	--	92.9	--	2.8	--	Gribanov (1948)
Kyrganik River	--	Tr.	--	93.6	Tr.	--	--	6.4	--	--	--	Gribanov (1948)
Paratunka River	--	Tr.	--	57.4	Tr.	--	--	42.6	--	--	--	Gribanov (1948)
Avachin Gulf, Solevarka Bay	--	Tr.	--	80.2	Tr.	--	--	19.8	--	--	--	Gribanov (1948)
Kalyger River	--	Tr.	--	27.5	Tr.	--	--	72.5	--	--	--	Gribanov (1948)
West coast of Kamchatka, USSR:												
Kikhchik River	--	Tr.	--	100.0	Tr.	--	--	--	--	--	--	Gribanov (1948)
Bolshaya River	--	--	Tr.	69.3	Tr.	--	--	30.1	--	--	--	Godfrey (1965); Gribanov (1948); Semko (1954)
Ozernaia River	--	--	Tr.	100.0	Tr.	--	--	--	--	--	--	Gribanov (1948)
Kukhtui River (Okhotsk)	--	--	--	32.8	--	--	--	67.2	--	--	--	Godfrey (1965)

[1] Logan, Sidney M. 1963. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1962-63, Vol. 4: 175-194, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[2] Logan, Sidney M. 1964. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 133-151, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[3] The high percentage of age 3_2 fish is atypical and not representative of Resurrection Bay streams. Dairy Creek juveniles are reared in a brackish water lagoon rather than in the stream itself, resulting in 1-year smolts. (Personal communication, Sidney Logan, Area Management Biologist, Alaska Department of Fish and Game, Soldotna, Alaska, March 15, 1971.)

[4] Collected by author in 1966.

Fifty-seven percent of the Karluk fish had migrated in their third year and 42% in their fourth year; only 1% had migrated in their fifth year (Table 1). Although the freshwater residence of fish in the Karluk escapement varied from 2 to 4 years, Karluk coho salmon, like those in all other systems, returned to spawn after being at sea for 12 to 18 months.

The presence of large numbers of fish (42%) that had spent 3 years in freshwater residence (age class 5_4) is unique to the Karluk system. Fish of age class 5_4 have been found in other Alaska river systems, i.e., the Yukon River (Gilbert, 1922), Resurrection Bay and Bear Creek (see footnotes 1 and 2, Table 1), Hood Bay Creek (Armstrong, 1970), Sashin Creek and Port Herbert (Crone, 1968), and Chignik River (Israel, 1933); but the proportion of 5_4 fish in the total runs to these systems is small—usually less than 5% (Table 1).

The age composition of stocks of coho salmon from systems on the Kamchatka Peninsula,

USSR, is similar to that of coho salmon in the northern areas of the west coast of North America. The main age classes are 3_2 and 4_3 (Table 1). The ratio of one age class to the other varies, however, from year to year and from area to area (Gribanov, 1948; Semko, 1954).

An additional comparison of the age composition of coho salmon from northern to southern latitudes is shown in Figure 2, which gives the percent age composition of the major age classes from five geographical areas along the west coast of North America. In California, the southern limit of the range of coho salmon, the major age class is 3_2, but jack salmon (age 2_2) contribute significantly to the runs. The 3_2 age class is still dominant in Washington, but the number of jack salmon is less and 4_3 fish are starting to appear. North of Washington to central British Columbia, more than 95% of the fish are age 3_2, and there are only traces of other age classes, mainly the 4_3 class. From central British Columbia and northward through Alaska, the primary age class is 4_3; 3_2 fish are the secondary class and 5_4 fish are found in small numbers. In Alaska, the increase in total age is the result of juvenile coho salmon residing an additional year in fresh water before migrating to sea. Possible exceptions to the dominance of the 4_3 age class in Alaska are the Ketchikan River, Dairy Creek, Yukon River, and Karluk River systems (Table 1). In the first three river systems, 3_2 fish are the dominant age class and 4_3 fish the secondary class. The sizes of the samples from these systems were small, however (less than 25 fish). In the Karluk system, although 4_3 fish were dominant, 5_4 fish rather than 3_2 fish were the secondary age class (Figure 2).

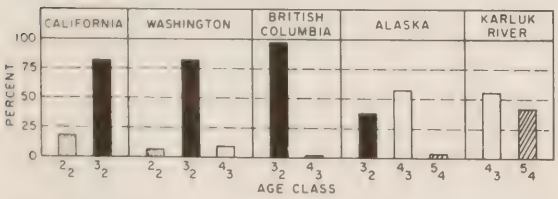

FIGURE 2.—Average age composition of coho salmon runs along the west coast of North America by geographical area (minor age classes omitted).

The presence of older fish (5_4) in northern latitudes may be a result of the juveniles being reared in lakes rather than rivers. Typically, coho salmon spawn in rivers or tributaries to rivers and the emerging fry reside in these areas until they migrate to sea. In contrast, in some Alaska river systems where 5_4 fish are part of the run (Table 1 and Figure 2), the juveniles migrate from spawning grounds to lakes before migrating to sea. It appears that some of the juveniles that reside in lakes (lake type) go to sea at an older age than those that reside in rivers (river type).[4]

NUMBER AND SIZE OF EGGS

In this section, information is presented on fecundity (number of eggs contained in a female) as a function of latitude and length, the relative numbers of eggs in right and left ovaries, and egg size in relation to length and fecundity. Fecundity and factors related to it form the basis for determining the reproductive potential of a spawning stock and subsequent survival from egg to young. Knowledge of variations in fecundity and egg size is of increasing importance in fish stocking and fish rehabilitation programs. Size of egg may be useful in predicting the condition, or hardiness, of developing fry. Because the fecundity of fish differs among geographic areas, the reproductive potential must be determined for each stock.

FECUNDITY AS A FUNCTION OF LATITUDE

The average fecundity for both North American and Asiatic stocks of coho salmon is considerably higher in fish from northern latitudes than in those from southern latitudes (Table 2 and Figure 3). Coho salmon from Alaska river systems (with the exception of the two small samples from Port Herbert and Sashin Creek)

[4] Personal communication, 1969, Charles J. DiCostanzo, Chief, Salmon Investigations, National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821.

TABLE 2.—Average fecundity of coho salmon stocks from North American and Asiatic river systems, arranged geographically from north to south.

Area	Latitude	Average number of eggs	Reference
North America			
Swanson River, Alaska	61° N	3,378	Engel (1966)[1]
Bear Creek, Alaska	60° N	4,115	Lawler (1963,[2] 1964[3])
Dairy Creek, Alaska	60° N	4,177	Engel (1965),[4]; Lawler (1963)[2]
Karluk River, Alaska	57° N	4,706	Present study
Pasagshak River, Alaska	57° N	4,510	Marriott (1968)[5]
Sashin Creek, Alaska	56° N	2,868	Crone (1968)
Port Herbert, Alaska	56° N	2,565	Crone (1968)
Namu River, British Columbia	54° N	3,002	Foerster and Pritchard (1936)
Fraser River, British Columbia	53° N	3,152	Foerster and Pritchard (1936)
Nile Creek, British Columbia	49° N	2,310	Wickett (1951)
Cultus Lake Hatchery, British Columbia	49° N	2,300	Foerster and Ricker (1953)
Port John, British Columbia	49° N	2,313	Hunter (1948)
Cowichan River, British Columbia	48° N	2,329	Neave (1948)
Oliver Creek, British Columbia	48° N	2,267	Foerster (1944)
Beadnell Creek, British Columbia	48° N	2,789	Foerster (1944)
Seattle, Wash.	47° N	3,141	Allen (1958)
Minter Creek, Wash.	47° N	2,447	Salo and Bayliff (1958)
Fall Creek, Alsea River, Ore.	44° N	1,983	Koski (1966)
Scott Creek, Calif.	37° N	2,336	Shapovalov and Taft (1954)
Asia			
East coast of Kamchatka, USSR:			
Ushki Hatchery	56° N	5,282	Gribanov (1948)
Kamchatka River	56° N	4,883	Gribanov (1948)
Paratunka River	53° N	4,350	Gribanov (1948)
West coast of Kamchatka, USSR:			
Bolshaya River	53° N	4,638	Semko (1954)
Sakhalin Island, USSR:			
Tymi River	52° N	4,570	Smirnov (1960)

[1] Engel, Larry J. 1966. Egg-take investigations in Cook Inlet drainage and Prince William Sound. *In* Federal aid in fish restoration, 1965-66 progress report, Vol. 7: 109-116, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[2] Lawler, Robert E. 1963. Silver salmon egg taking investigations in Cook Inlet drainage. *In* Dingell-Johnson project report, 1962-63, Vol. 4: 161-173, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[3] Lawler, Robert E. 1964. Egg take investigations in Cook Inlet and Prince William Sound. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 123-132, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[4] Engel, Larry J. 1965. Egg take investigations in Cook Inlet drainage and Prince William Sound. *In* Dingell-Johnson project report, 1964-65, Vol. 6: 155-163, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

[5] Marriott, Richard A. 1968. Inventory and cataloging of the sport fish waters in southwest Alaska. *In* Federal aid in fish restoration, 1967-68 progress report, Vol. 9: 81-93. Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)

are more fecund than coho salmon from more southerly areas in North America (Figure 3). Stocks of coho salmon from Asiatic river systems are extremely fecund, even more so than North American stocks in more northerly latitudes. The high fecundity of Karluk River coho salmon more closely resembles the fecundity of Asiatic stocks than North American ones.

Contrary to these findings for coho salmon, Rounsefell (1957) suggests that for the genus *Oncorhynchus*, salmon in southern latitudes may be more fecund than those in northern latitudes because of ". . . the higher age at maturity, and therefore slower growth rates, from south to north." Rounsefell found that the amount of time juvenile sockeye salmon spent in fresh water had no effect on fecundity, but the amount of time the adults spent at sea did have an effect: adult sockeye salmon that spent 2 years at sea had higher fecundity counts than fish of the same size that spent 3 years at sea. With coho salmon, however, the greater age at maturity is not due to increased time in the ocean but to increased time in fresh water.

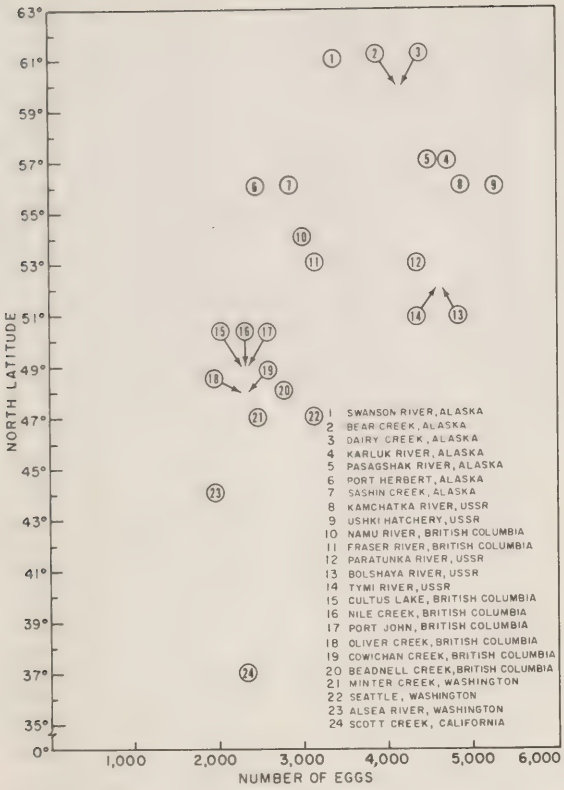

FIGURE 3.—Average fecundity of various stocks of coho salmon from North America and Asia.

FECUNDITY AS A FUNCTION OF LENGTH

The presence of a positive relation between fecundity and length in the genus *Oncorhynchus* is well known (Gilbert and Rich, 1927; Foerster and Pritchard, 1941; Allen, 1958; Hartman and Conkle, 1960). For fish in general, the relation of fecundity to length is logarithmic ($\hat{Y} = aX^b$) over a wide range of lengths. For salmon, however, the narrow range in length at maturity permits this relation to be described adequately by a straight line of the form $\hat{Y} = a + bX$ (Foerster and Pritchard, 1941; Rounsefell, 1957).

I counted the total number of eggs in 49 coho salmon from the Karluk River and calculated the relation between number of eggs and mideye-fork length by the method of least squares. The result may be expressed by the equation $\hat{Y} = -7{,}503.55 + 195.51X$, where $\hat{Y}$ is the estimate of number of eggs and X is the mideye-fork length of female salmon (Figure 4). The mean number of eggs for the sample was 4,706 (range 1,724 to 6,906); the mean length was 62.1 cm (range 46.6 to 69.8 cm).

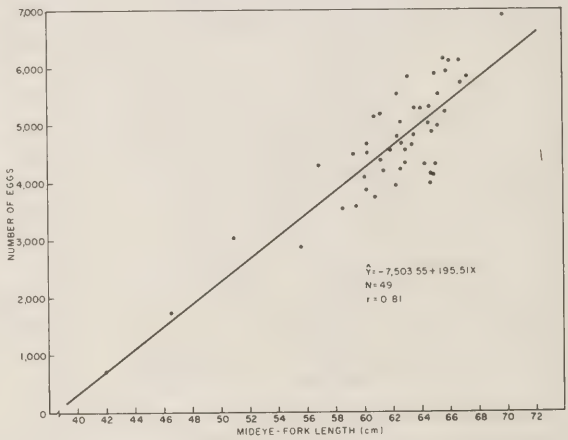

FIGURE 4.—Relation of fecundity to length of coho salmon sampled at Karluk weir, 1966.

It is difficult to determine if the high fecundity of coho salmon of the Karluk system (Figure 3) is due to greater fecundity per unit length or simply to the fact that coho salmon from Karluk are very large. The average lengths of female coho salmon from various spawning streams along the Pacific coast of North America are quite variable and do not seem to follow any set geographic pattern (Table 3). Moreover, Karluk fish were measured from mideye to fork of tail, and direct comparisons of lengths with coho salmon from other areas are difficult to make because of variability in the types of measurements used. For instance lengths reported from areas other than Karluk include tip of snout to fork of tail (fork length), tip of snout to tip of tail (total length), and tip of snout to base of tail (standard length).

TABLE 3.—Average lengths of female coho salmon from river systems along the Pacific coast of North America and Asia, arranged geographically from north to south.

Area	Average length				Reference
	Fork	Total	Standard	Mideye-fork	
	cm	*cm*	*cm*	*cm*	
North America					
Yukon River, Alaska	63.4	--	--	--	Gilbert (1922)
Swanson River, Alaska	62.0	--	--	--	Engel (1966)[1]
Resurrection Bay, Alaska	67.2	--	--	--	Logan (1965)[2]
Dairy Creek, Alaska	72.8	--	--	--	Engel (1965)[3]
Brooks River, Alaska	--	58.8	--	--	(4)
Karluk River, Alaska	--	--	--	62.1	Present study
Sashin Creek, Alaska	70.5	--	--	--	Crone (1968)
Port Herbert, Alaska	67.8	--	--	--	Crone (1968)
Namu River, British Columbia	--	69.0	--	--	Foerster and Pritchard (1936)
Fraser River, British Columbia	--	64.0	--	--	Foerster and Pritchard (1936)
Seattle, Wash.	63.4	--	--	--	Allen (1958)
Minter Creek, Wash.	--	--	62.1	--	Salo (1955)
Columbia River, Wash.	74.6	--	--	--	Marr (1943)
Deer Creek, Oreg.	70.7	--	--	--	Koski (1966)
Flynn Creek, Oreg.	69.4	--	--	--	Koski (1966)
Needle Branch, Oreg.	67.6	--	--	--	Koski (1966)
Scott Creek, Calif.	66.3	--	--	--	Shapovalov and Taft (1954)
Waddell Creek, Calif.	63.9	--	--	--	Shapovalov and Taft (1954)
Asia					
East coast of Kamchatka, USSR:					
Kamchatka River	60.9	--	--	--	Gribanov (1948)
Kyrganik River	68.1	--	--	--	Gribanov (1948)
Kalyger River	61.0	--	--	--	Gribanov (1948)
Avachin Gulf	55.4	--	--	--	Gribanov (1948)
Paratunka River	59.4	--	--	--	Gribanov (1948)
West coast of Kamchatka, USSR:					
Kikhchik River	58.6	--	--	--	Gribanov (1948)
Bolshaya River	57.4	--	--	--	Gribanov (1948)
Ozernaia River	62.6	--	--	--	Gribanov (1948)

[1] See footnote 1, Table 2.
[2] Logan, Sidney M. 1965. Silver salmon studies in the Resurrection Bay area. *In* Dingell-Johnson project report, 1964-65, Vol. 6: 129-145, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[3] Lawler, Robert E. 1964. Egg take investigations in Cook Inlet and Prince William Sound. *In* Dingell-Johnson project report, 1963-64, Vol. 5: 123-132, Alaska Dep. Fish Game, Sport Fish Div., Juneau, Alaska. (Unpublished.)
[4] Eicher, George J., Jr. The effects of laddering a falls in a salmon stream. National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska, 5 p. (Unpublished.)

NUMBER OF EGGS IN RIGHT AND LEFT OVARIES

The numbers of eggs in the right and left ovaries of the genus *Oncorhynchus* are usually quite variable. Rounsefell (1957) noted that although the rate of maturation of eggs from Karluk Lake sockeye salmon was the same in both ovaries of the same fish, the number of eggs in each ovary varied. Eguchi and his co-workers (Rounsefell, 1957) found no significant differences in the numbers of eggs in the two ovaries in chum salmon, *O. keta*, in Japanese waters. Helle (1970) found the same lack of a significant difference in a sample of pink salmon, *O. gorbuscha*, from Olsen Bay, Alaska, in 1963. Sockeye salmon from Brooks Lake, Alaska, in 1957 and 1958 and from Karluk Lake in 1958 had more eggs in the left ovary than in the right (Hartman and Conkle, 1960). At Bare Lake, Alaska, sockeye salmon had more eggs in the right ovary than in the left (Nelson, 1959).

I compared the numbers of eggs from the right and left ovaries of Karluk River coho salmon (Table 4) by means of a t test for paired observations. The differences between the numbers of eggs in the right and left ovaries were significant ($t = 2.60$; df $= 31$; $P = 0.05$). In 31 fecundity samples, 71% had more eggs in the right ovary than the left. I could not find comparable information on comparisons between the numbers of eggs in the ovaries of coho salmon from other areas.

TABLE 4.—Numbers of eggs in right and left ovaries from coho salmon collected at the outlet to Karluk Lake, 1966.

Sample number	Mideye-fork length (cm)	Number of eggs		
		Right ovary	Left ovary	Total
1	50.9	1,640	1,403	3,043
2	61.4	2,265	1,918	4,183
3	65.0	3,005	2,876	5,881
4	56.9	2,213	2,083	4,296
5	62.7	2,322	2,337	4,659
6	65.6	3,001	3,147	6,148
7	69.8	3,559	3,347	6,906
8	64.7	2,258	1,884	4,142
9	62.6	2,546	2,501	5,047
10	60.2	2,433	2,220	4,653
11	59.3	2,243	2,225	4,468
12	60.2	2,331	2,161	4,492
13	62.3	2,481	2,283	4,764
14	61.2	2,620	2,539	5,159
15	60.1	2,067	2,000	4,067
16	63.5	2,581	2,221	4,802
17	64.5	2,473	2,546	5,019
18	67.2	2,604	3,233	5,837
19	60.2	2,044	1,813	3,857
20	65.2	2,824	2,697	5,521
21	64.0	2,608	2,659	5,267
22	65.1	2,491	2,501	4,992
23	66.0	2,926	3,174	6,100
24	62.9	2,266	2,280	4,546
25	65.8	3,047	2,878	5,925
26	64.6	2,726	2,579	5,305
27	63.6	2,721	2,563	5,284
28	66.7	3,104	2,997	6,101
29	63.1	2,981	2,843	5,824
30	61.9	2,176	2,125	4,301
31	64.8	2,340	2,521	4,861
Average	63.0	2,545	2,469	5,015

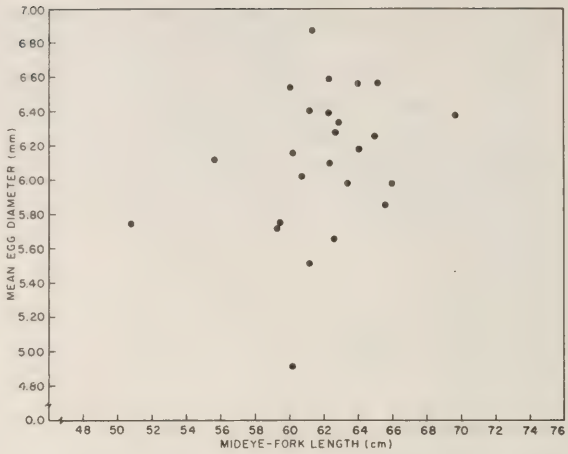

FIGURE 5.—Relation of mean egg diameter to mideye-fork length of female coho salmon, Karluk River, 1966.

RELATION OF EGG SIZE TO LENGTH AND TO FECUNDITY

The average diameter of eggs obtained from the fecundity samples from Karluk River was plotted against the length of the female coho salmon from which the samples were taken (Figure 5) to determine if there was a relation between the size of a female and the size of her eggs. The size of eggs increases as they mature, and so the eggs used had to be in the same stage of maturation. I therefore selected only females beginning to show secondary sexual characteristics and containing eggs that could not be readily expressed from the body cavity. For 25 females the eggs varied in size from 4.92 to 6.88 mm (mean 6.11 mm); lengths varied from 50.4 to 69.8 cm (mean 62.0 cm). No relation was found between the size of the egg and the length of the fish. Allen (1958) in his studies of coho salmon in Green River, Wash., also found no relation.

The average diameters of eggs were plotted against number of eggs in individual fish to determine if a relation existed between the fecundity of a female and the size of her eggs (Figure 6). For 24 females, the egg diameter ranged

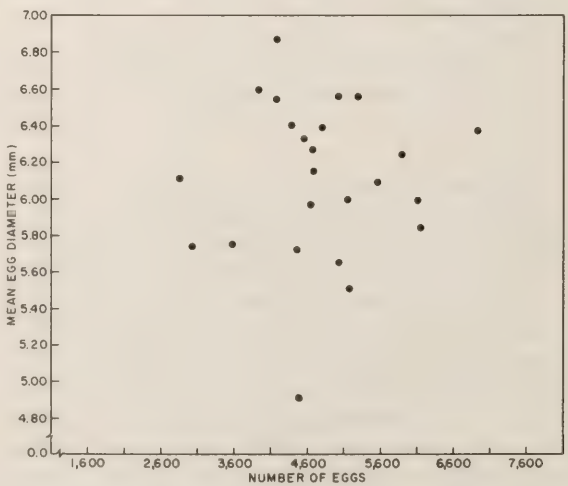

FIGURE 6.—Relation of mean egg diameter to number of eggs in female coho salmon, Karluk River, 1966.

from 4.91 to 6.87 mm (mean 6.11 mm); fecundity ranged from 2,855 to 6,906 (mean 4,766). No relation was found: eggs from a female with low fecundity were not necessarily large, nor were those from a female with high fecundity necessarily small. Allen (1958) reported similar findings.

Unlike the general relation that exists between fecundity and length (i.e., larger fish are more fecund), the size or fecundity of the females I sampled apparently had no relation to the size of the eggs. Large, fecund females had a wide range of egg sizes (Figure 5). Thus, the larger number of eggs in large females may be due to a larger body cavity that allows more eggs to develop rather than to the fish having smaller eggs.

COHO SALMON SMOLTS

Smolts of coho salmon, like those of other salmon that live for a while in fresh water before migrating to sea, migrate seaward at a particular season and under particular light intensities. This migration and the associated environmental factors and information on age and size of migrating smolts are discussed in this section.

SEASONAL MIGRATION

Coho salmon juveniles reside in Karluk Lake for 1 to 4 years before they migrate to sea as smolts. From 1961 to 1967 the migration began in mid-May and was usually over by early July (Figure 7).

Although most coho salmon migrate in the spring (Hamilton and Andrew, 1954; Taft, 1934; Gharrett and Hodges, 1950; Semko, 1954), several exceptions do exist. In the Paratunka River, Kamchatka Peninsula, the migration extends from the end of May to the end of August (Gribanov, 1948); in several streams in Oregon it extends from late winter to May (Chapman, 1961); in some streams in western Washington it runs from early winter to late spring (Smoker, 1953); and at Waddell Creek, Calif., small numbers of atypical migrants migrate in the fall and early winter (Shapovalov and Taft, 1954). The

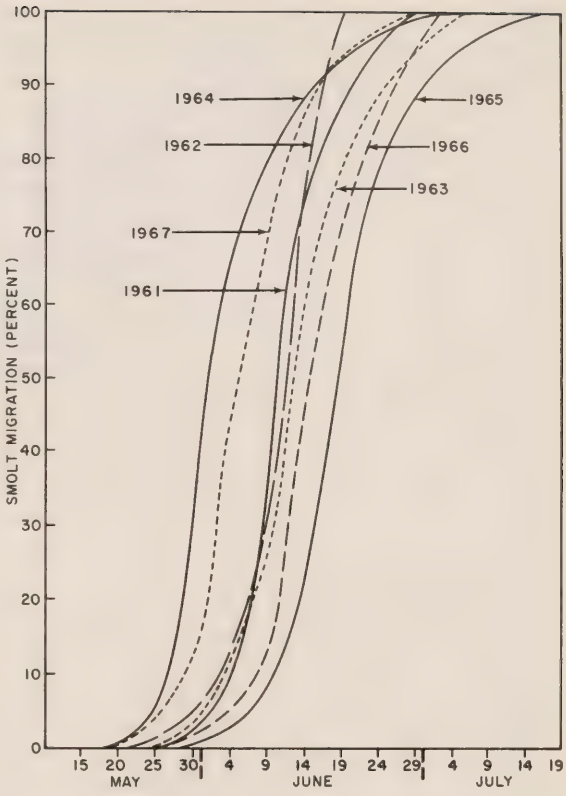

FIGURE 7.—Cumulative seasonal migration of coho salmon smolts from Karluk Lake, 1961-67.

number of coho salmon smolts involved in the early or late parts of these migrations, however, represents only a small percentage of the total number of smolts in each migration.

The warming of the water after the ice breaks up is of major importance in initiating the seaward migration of smolts. Hartman, Heard, and Drucker (1967) found this to be a major factor in the migration of sockeye salmon in lakes of southwestern Alaska; and Logan (see footnote 2, Table 1) found that the coho salmon smolt migration in Bear Lake, Alaska, did not start until the ice cover on the lake was gone and the water temperature had risen to 4.2° C. Ninety percent of the Bear Lake coho salmon smolts had migrated to sea when water temperatures ranged between 5° and 13.3° C. Coho salmon smolts apparently migrate over a greater

temperature range than sockeye salmon, whose migration generally ends when water temperatures reach about 10° C (see footnote 2, Table 1).

At Karluk Lake, for each year from 1961 to 1968 (excluding 1964) the date by which 50% of the coho salmon smolts had migrated was later than the comparable date for sockeye salmon smolts (Table 5). The difference in time of the two migrations ran from 6 to 19 days (average 11 days). Not only did more of the coho salmon smolts migrate later than the sockeye salmon smolts, but the coho salmon smolts usually migrated during a period of relatively warmer water, when the abundance of migrating sockeye salmon smolts had greatly diminished. Similarly, Foerster and Ricker (1953) found that the coho salmon smolt migration in Cultus Lake and Sweltzer Creek, British Columbia, always followed the sockeye salmon smolt migration by about 10 days.

Although the seasonal timing of the outmigration of coho salmon smolts may vary from system to system, it is relatively consistent within a particular system. When time of migration is plotted against latitude, a definite south to north cline in time of migration becomes evident (Figure 8). Coho salmon smolts migrate later in the season in northerly systems than in more southerly ones. More than a month separates the midpoint of smolt migration from the central coast of California (lat 37° N) to the Gulf of Alaska (lat 60° N). This relation also applies for the Asiatic side of the Pacific Ocean.

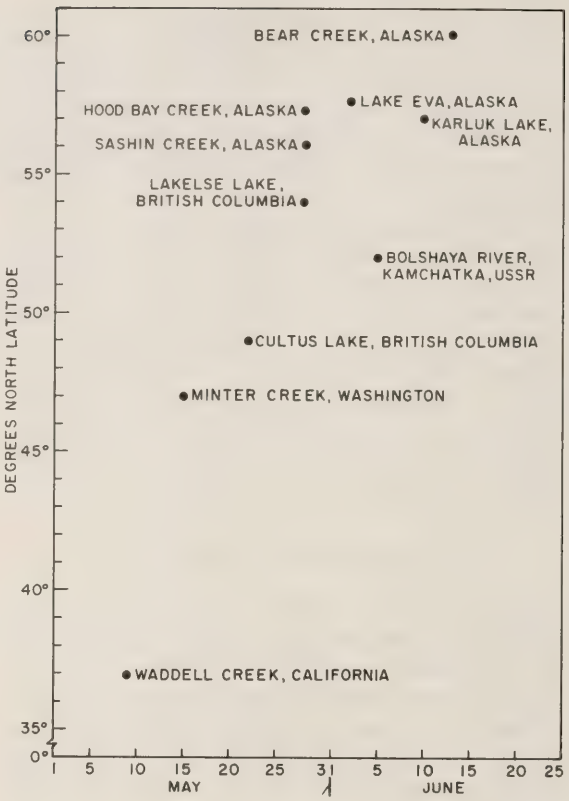

FIGURE 8.—Average date when 50% of the coho salmon smolts had migrated from river and lake systems along the Pacific coast of North America and Asia.

DIEL PATTERN OF MIGRATION

The transformation of juvenile coho salmon from either lake- or stream-type residents to smolts is associated with avoidance of light and increasing nocturnal activity (Hoar, Keenleyside, and Goodall, 1957; Hoar, 1958; Smirnov, 1960).

TABLE 5.—Dates by which 50% of the coho and sockeye salmon smolts migrated from Karluk Lake, 1961-68.

Year	Sampling period	50% migration date	
		Coho salmon	Sockeye salmon
1961	May 25 to June 29	June 10	June 2
1962	May 17 to June 21	June 10	May 29
1963	May 18 to July 6	June 12	June 6
1964	May 17 to July 6	June 2	June 3
1965	May 16 to July 16	June 18	June 6
1966	May 18 to July 2	June 15	June 4
1967	May 18 to June 29	June 5	May 27
1968	May 17 to June 26	June 12	May 24

Although most of the migration of smolts to salt water occurs during the darkest hours of the night, some occurs during the daytime. At Karluk Lake, for instance, during some years almost 40% of the coho salmon smolts migrated in the daytime—between 0600 and 1800 hr (Figure 9). In other coho salmon rivers, the percentage of smolts that migrate seaward during daylight is quite variable. In the Bolshaya River in Kamchatka, during the years 1944-47, 6.3 to 50.0% of the age 1 smolts[5] and 8.8 to 73.2%

[5] Fish that go to sea in their second year.

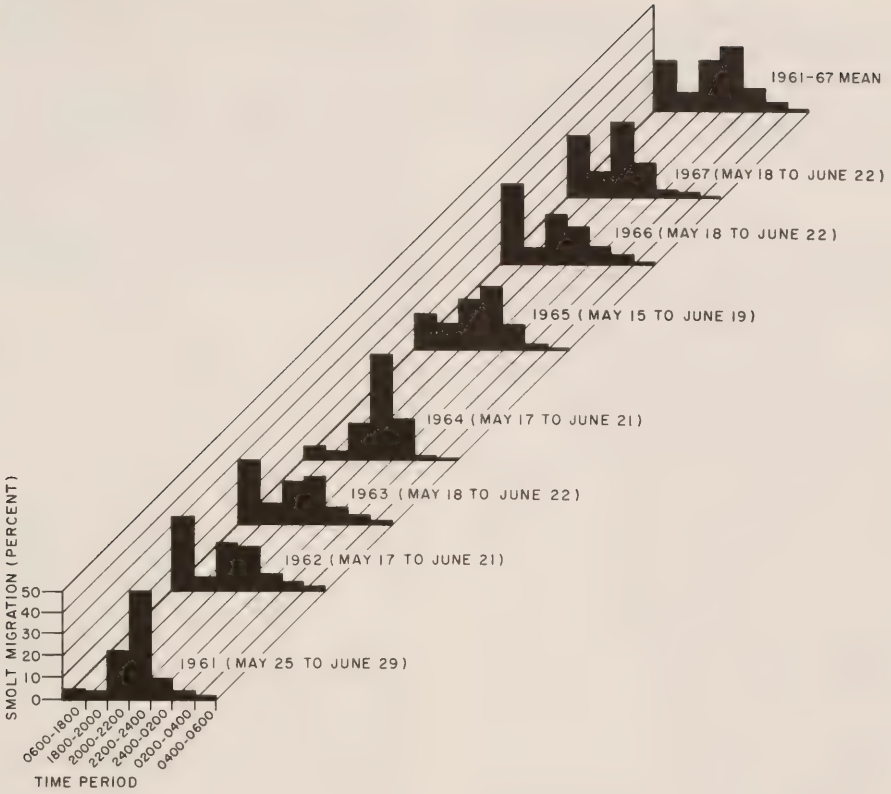

FIGURE 9.—Migration of coho salmon smolts by time period from Karluk Lake for the years 1961-67.

of the age 2 smolts migrated in daylight (Semko, 1954.) At Bear Creek, Alaska, 49.8% of the smolts migrated between 0400 and 2000 hr in 1962 (see footnote 1, Table 1), and 16% migrated between 0900 and 1700 hr in 1964 (see footnote 2, Table 3).

AGE

In 1956, 1965, and 1968, scale samples taken from seaward-migrating coho salmon smolts at the Karluk Lake weir revealed that the dominant ages were 2 and 3 and that the age composition was similar between years (Table 6).

The freshwater age composition determined from the scales of adults collected in 1966 was strikingly similar to the age composition of seaward-migrating smolts in 1965—smolts that produced the adults in 1966 (Table 6). The only group missing from the adult scale sample but present in small numbers in the smolt scale samples was age 1 (fish that went to sea in their second year of life). Fish from this age class could have been missing in the returning adults

TABLE 6.—Freshwater age composition of Karluk Lake coho salmon as determined from smolt and adult scale samples.

Freshwater age	Percent composition			
	From smolt scales			From adult scales
	1956	1965	1968	1966
1	1.4	3.0	3.0	--
2	44.5	51.5	48.5	56.9
3	49.1	43.9	42.5	41.7
4	4.9	1.5	6.0	1.4

because (1) they had poor ocean survival because of their small size; (2) the young overwintered in the river and migrated as age 2 smolts the following year; or (3) the young never migrated at all.

SIZE

Only lengths were measured in 1956, and lengths and weights were taken in 1965 and 1968. A summary of average size data by age class is presented in Table 7. Average lengths for comparable age classes were greater in 1968 than in 1956 and 1965. Average weights, with the exception of age 3 fish, were less in 1968 than 1965. Differences in lengths and weights between smolts for the two comparable years (1965 and 1968) are reflected in the condition factor (K), or coefficient of condition, which indicates the relative well-being of the fish. In 1965 all age groups had K values greater than 1.0000; the range was 1.0544 to 1.3695. In 1968 all K values were under 1.0000; the range was 0.9187 to 0.9600.

Information on the size of coho salmon smolts from other spawning systems is presented in Table 8. This table gives information for natural or "wild" populations and not for artificially hatched or reared stocks. Karluk Lake coho salmon smolts were generally as large as smolts of the same age from other areas or larger.

POSSIBLE EFFECTS OF INCREASED FRESHWATER RESIDENCE ON SURVIVAL OF COHO SALMON

The extended period of freshwater residence resulting in coho salmon smolts of age 3 occurs in many systems but seems to be significant only at Karluk.

It is interesting to hypothesize what effect a prolonged freshwater residence has on the annual return of adult coho salmon at Karluk Lake. Is an increased freshwater residence advantageous or disadvantageous to survival of each year class? What effect is there on marine survival of coho salmon if they take up ocean residence at an older age and consequently a larger size?

One means of answering these questions is to examine freshwater and marine survival rates for coho salmon from other areas. Survival from egg to smolt (fresh water) and smolt to returning adult (marine) are shown in Table 9 for some areas in California, Oregon, Washington, and British Columbia. Both freshwater and marine survival for age 1 smolts from these areas are quite variable: 0.13 to 12.00% and 3.77 to 11.79% respectively. The survival data in Table 9 pertain to stocks in which the smolts were primarily age 1 when they migrated to sea, and the application of these data to more northern stocks in which the smolts are mostly older and larger when they migrate must be done with caution.

The small population of age 2 smolts from Sweltzer Creek in British Columbia (Table 9) is of interest because these fish are more comparable to Karluk smolts, in that they may possibly have had a period of lake residence. Marine survival of these older, larger fish was high. Of 72 fin-clipped migrating age 2 smolts, 19 (26%) returned 5 or 6 months later as 3_3 fish (Foerster and Ricker, 1953). Although marine survival for these age 2 smolts might have been lower if they had spent another year in the ocean, it

TABLE 7.—Average length, weight, and condition factor of coho salmon smolts by age from Karluk Lake, 1956, 1965, and 1968.

Age	1956			1965			1968		
	Length	Weight	Condition factor	Length	Weight	Condition factor	Length	Weight	Condition factor
	mm	*g*		*mm*	*g*		*mm*	*g*	
1	106.8	--	--	112.5	19.5	1.3695	114.8	13.9	0.9187
2	139.7	--	--	136.3	28.2	1.0544	140.1	26.4	0.9600
3	151.1	--	--	141.7	30.7	1.0790	160.4	38.5	0.9329
4	165.4	--	--	177.0	63.9	1.1523	181.8	56.2	0.9353

TABLE 8.—Average fork lengths of coho salmon smolts of ages 1 to 4 from river and lake systems along the Pacific coast of North America and Asia, arranged geographically from north to south.

Area and year	Age				Reference
	1	2	3	4	
	mm	*mm*	*mm*	*mm*	
North America					
Hood Bay Creek, Alaska					
1968	83.0	96.0	--	--	Armstrong (1970)
1969	79.0	91.0	--	--	Armstrong (1970)
Karluk River (Karluk Lake), Alaska					
1956	106.8	139.7	151.1	165.4	Present study
1965	112.5	136.3	141.7	177.0	Present study
1968	114.8	140.1	160.4	181.8	Present study
Bear Creek, Alaska					
1962	106.3	118.7	150.8	--	Logan[1]
Sweltzer Creek (Cultus Lake), British Columbia					
--	110-120	--	--	--	Foerster and Ricker (1953)
1939	--	291.6	--	--	Foerster and Ricker (1953)
Minter Creek, Wash.					
1940	[2]96.3	--	--	--	Salo and Bayliff (1958)
1953	[2]99.7	--	--	--	Salo and Bayliff (1958)
Deer Creek, Oreg.					
1960	88.7	--	--	--	Chapman (1961)
Flynn Creek, Oreg.					
1960	88.1	--	--	--	Chapman (1961)
Waddell Creek, Calif.					
1933	113.5	--	--	--	Shapovalov and Taft (1954)
1934	113.3	--	--	--	Shapovalov and Taft (1954)
1935	113.1	--	--	--	Shapovalov and Taft (1954)
1936	116.6	--	--	--	Shapovalov and Taft (1954)
1937	114.8	--	--	--	Shapovalov and Taft (1954)
1938	112.4	--	--	--	Shapovalov and Taft (1954)
1939	112.4	--	--	--	Shapovalov and Taft (1954)
1940	109.5	--	--	--	Shapovalov and Taft (1954)
1941	103.1	--	--	--	Shapovalov and Taft (1954)
Asia					
Bolshaya River, Kamchatka, USSR					
--	85.0	130.0	--	--	Semko (1954)

[1] Personal communication, Sidney M. Logan, Fishery Biologist, Alaska Department of Fish and Game, May 3, 1967.
[2] Primarily age 1 fish.

TABLE 9.—Average freshwater and marine survival for coho salmon from various streams along the Pacific coast of North America, arranged geographically from north to south.

Streams	Percent survival		Reference
	Fresh water	Marine	
	Egg to age 1 smolt	Age 1 smolt to adult	
Nile Creek, British Columbia	1.40	6.00	Wickett (1951)
Hooknose Creek, British Columbia	1.30	11.79	Godfrey (1965)
Sweltzer Creek, British Columbia	[1]0.13	8.07	Foerster and Ricker (1953)
Sweltzer Creek, British Columbia	[2,3]0.33	--	Foerster and Ricker (1953)
Sweltzer Creek, British Columbia	--	[4]26.39	Foerster and Ricker (1953)
Minter Creek, Wash.	3.22	3.77	Salo and Bayliff (1958)
Deer Creek, Oreg.	12.00	--	Chapman (1961)
Waddell Creek, Calif.	1.35	4.95	Shapovalov and Taft (1954)

[1] Before piscivorous fishes were controlled.
[2] After piscivorous fishes were controlled.
[3] Geometric mean.
[4] Age 2 fish only.

nevertheless was considerably higher than for any of the age 1 smolts.

In the absence of knowledge of survival rates for the more northern populations of coho salmon, an examination of the effect of increased freshwater residence on sockeye salmon, the dominant species of salmon in the Karluk system, is of value. Sockeye salmon juveniles at Karluk Lake have long been known to reside in the lake a year or more longer than do sockeye salmon in other areas (Gilbert and Rich, 1927). In most Alaska systems, sockeye salmon smolts migrate at the beginning of their second or third year of life, but at Karluk Lake most sockeye salmon smolts migrate at the beginning of their third or fourth years. Possibly the factor(s) responsible for the 1-year holdover of juvenile sockeye salmon in the lake may also be responsible for the holdover of juvenile coho salmon.

Freshwater survival of sockeye salmon at Karluk Lake is extremely poor, but marine survival is good. During the late 1920's and early 1930's, freshwater survival was less than 1% and ocean survival was about 21% (Barnaby, 1944). In recent years, freshwater survival has dropped to less than 0.5% and ocean survival has increased to about 40%.[6] Ricker (1962) modified Barnaby's data by applying a marking mortality factor derived from his Cultus Lake studies and determined that the older, larger smolts have greater marine survival and that Barnaby's original estimate of 21% survival was too low. Average marine survival by freshwater age for the years 1926 and 1929-33 were as follows: age 1 smolts, 18.3%; age 2, 27.4%; age 3, 34.2%, and age 4, 33.3%. Ricker attributed the high ocean survival to the large size of the smolts when they entered salt water. The larger size of the sockeye salmon smolts at the time of seaward migration, however, is offset by a greater total freshwater mortality due to their prolonged stay in the lake.

I have shown that in the more northern latitudes coho salmon usually reside a minimum of one extra year in fresh water before they migrate to sea. Generally, a longer period of freshwater residence will result in greater freshwater mortality but lower marine mortality because the fish are larger when they enter the ocean. Most likely, as with Karluk Lake juvenile sockeye salmon, an extra year in the lake for juvenile coho salmon probably results in a greater total freshwater mortality. Total marine mortality, however, may be less for coho salmon than for sockeye salmon because the coho salmon generally spend less time at sea before returning to spawn (12 to 18 months rather than 24 to 30 months).

[6] Unpublished data on file at National Marine Fisheries Service Auke Bay Fisheries Laboratory, Auke Bay, Alaska 99821.

SUMMARY AND CONCLUSIONS

Both the freshwater and total ages of adult coho salmon increase from southern to northern latitudes. In California, the southern portion of the coho salmon's range, fish of ages 3_2 and 2_2 are in the majority, but in the northern areas, ages 4_3 and 3_2 predominate. Karluk coho salmon, however, are unique, in that although age 4_3 fish are still the primary age class, the age 3_2 fish are replaced by age 5_4, so that age 5_4 fish account for 42% of the run. In no other North American or Asiatic coho salmon stock for which information is available is such a large percentage of the run composed of 5_4 fish.

The increase in total age of coho salmon from south to north is associated with the increased time the juveniles spend in fresh water. The small numbers of age 5_4 fish in several Alaska stocks may represent juveniles that live in lakes rather than rivers.

Fecundity generally increases from south to north, and Karluk coho salmon are the most fecund of any North American stock and closely parallel the highly fecund Asiatic stocks from the Kamchatka Peninsula. In Karluk coho salmon, there is a relation between number of eggs and length but no relation between egg size and length or egg size and fecundity. Egg counts are significantly higher in the right ovary than in the left.

Coho salmon smolts generally migrate after the ice breaks up and the water warms. In North America, the migration is earlier in southern latitudes than northern ones. The coho salmon

migration at Karluk Lake is primarily nocturnal, although some daytime migration does occur.

A prolonged freshwater residence by juvenile coho salmon in Karluk Lake should result in a greater total freshwater mortality, but the resulting larger smolts should have a lower total marine mortality. Coho salmon at Karluk may have an even lower marine mortality than sockeye salmon, in part because the coho salmon spend less time at sea.

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DEVELOPMENTAL RATES AT VARIOUS TEMPERATURES OF EMBRYOS OF THE NORTHERN LOBSTER (*Homarus americanus* MILNE-EDWARDS)

HERBERT C. PERKINS[1]

ABSTRACT

The rates of development, time from extrusion to hatching at various temperatures, and differential developmental rates at the same temperature of lobster embryos are presented. The eyes of the embryos were measured to monitor the rates and degree of embryo development.

Herrick (1890, 1896) discussed developmental rates for lobster embryos in the early stages at 20° to 22° C. Templeman (1940) determined the times required at various temperatures for lobster eggs to reach the 16-cell stage, and up to the formation of eye pigment. The information from these studies is valuable for determining the rates of early development in lobster egg-embryos but is not adequate for the accurate assessment of developing embryos once eye pigment has been formed. By monitoring the rate of development of lobster embryos throughout the embryonic period at various temperatures one can predict hatching times of larvae and control hatching times by manipulating the water temperature in tanks holding egg-bearing females, so that larvae can be available over a wide period of time for use in experiments. This paper presents the rates of development and time required to complete the embryonic period by lobster embryos at various temperatures and a method of continually monitoring that development. The work was conducted at the National Marine Fisheries Service, Biological Laboratory, Boothbay Harbor, Maine, as part of the Laboratory's investigation of the early life history of the lobster.

METHODS AND MATERIALS

Most of the egg-bearing lobsters used in this study came from the offshore canyons of the continental shelf, south and east of New England. A few came from the Boothbay Harbor area and are so noted. All egg-bearing females were kept in tanks at seasonal water temperatures or in water warmed to various constant temperatures. Water from the laboratory's seawater system was piped to the heated tanks at rates consistent with the capacity of the heaters. Salinity averaged 31‰ and ranged from 29 to 32‰ throughout the study period.

Five egg-bearing females were kept in a tank through which natural seawater at seasonal temperature was circulated during the developmental period of their eggs. The purpose of holding these females at seasonal temperatures was to determine the rates of development of their embryos in a natural temperature regime. Fourteen female lobsters from the offshore canyons, with recently extruded eggs (eggs in prenaupliar condition), were kept at constant temperatures from 6.9° to 24.6° C. The primary objective at the higher temperatures (20°-24.6° C) was to force the eggs to hatch before the time they would do so at seasonal temperatures. Of further interest was the rate of development of the embryos at constant, rather than fluctuating, temperatures, and the time required for the eggs to hatch at these temperatures from a given point in their development.

The rates and extent of development of the embryos were determined by measuring the size of their eyes. Measurements were made to the nearest micron with an ocular micrometer in a dissecting microscope at a magnification of 50×. When measuring an eye, I took its greatest width and greatest length, combined these figures and

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divided by two. The resulting figure was used as an index of development only and was not meant to represent the actual increase or growth of the eye. Samples of 15 to 20 eggs were removed from the periphery of an egg mass whenever a measurement was desired (usually once a week). From these samples five eggs were selected randomly, and one eye of each embryo measured. A mean of these five measurements was used as a working figure or index. Eggs were taken from the peripheral layer of the mass as these are the furthest advanced in development and are the first to hatch. Variation in the eye measurements of eggs from this layer ranges from zero to 5%. When the eyes first appear and are large enough to measure, they are but thin crescents, darkly pigmented and surrounded by a halo of lighter material. The dark crescents only were measured. The eyes are very distinct for most of the developmental period and are easily measured, the crescents gradually becoming tear-drop in shape. The index of the eye is about 70μ when it is first measurable; the index is about 560μ at hatching. All eyes were measured after the eggs had been preserved in a 5% solution of Formalin in seawater. Preservation in Formalin caused significant swelling in the eggs themselves but had no determinable effect on the size of the eyes.

RESULTS AND DISCUSSION

TRENDS OF EMBRYONIC DEVELOPMENT IN WATER OF SEASONAL TEMPERATURES

The developmental patterns, from onset of eye pigment to hatching, of the embryos of the five females held at seasonal temperatures are shown in Figure 1, as is the cycle of water temperature for the same period. The trends of embryonic development were plotted by using periodic (usually weekly) measurements of the eye index of each egg mass. These five lobsters had extruded their eggs in the laboratory tanks so the age of each egg mass was known. From the latter part of November to the first of May of the following year, water temperatures were no higher than 6° C. Embryonic development during this period ceased in some of the egg masses and was barely discernible in others, at least by the method of eye index measurement. Squires (1970), using the amount of yolk material in the eggs as a criterion, reported a standstill in development during the winter in embryos of Newfoundland lobsters.

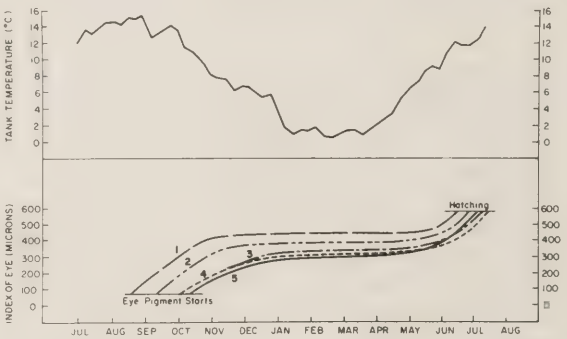

FIGURE 1.—Trends of development of the embryos of five female lobsters held in water of seasonal temperature at the Boothbay Harbor Laboratory and the temperature cycle during the period. The lines showing developmental trends are derived from plots of periodic measurements of the embryos' eye indices. The lines are numbered in accordance with the age of the egg mass; the lower the number, the older the egg mass.

DIFFERENTIAL RATES OF DEVELOPMENT

The developmental rates of lobster embryos appear to be governed not only by their thermal environment, but by the age or extent of development at which they are subjected to that environment. During the experiments I conducted the older or more advanced embryos developed at slower rates than those less advanced, though all were maintained in the same tank. The oldest egg mass of the five females held under seasonal conditions was extruded 7 weeks before the youngest, but the total time for development of the younger egg mass was 4½ weeks less than the older; the younger embryos had developed considerably faster. Measurements of the eye index of embryos in all five egg masses were made for the first time on November 7. In Fig-

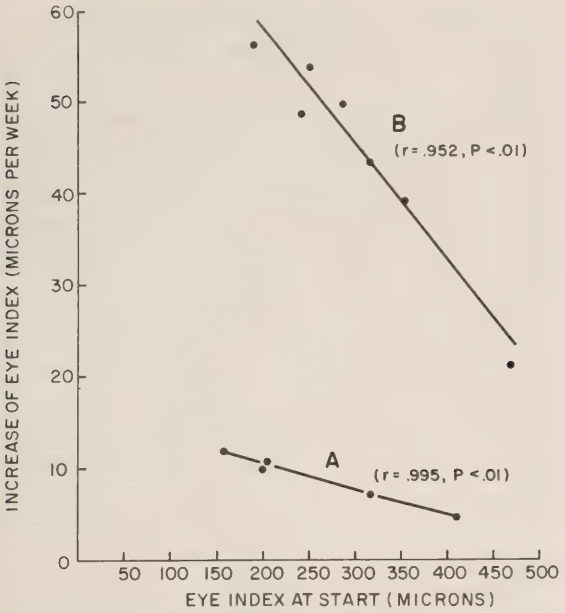

FIGURE 2.—Line A represents the different rates of increase of the eye index, in microns per week, of the embryos of the five lobsters held in the same tank, under seasonal conditions, from November 7, until hatching. Line B represents the different rates of eye increase of the embryos of seven females held at a constant temperature of 22.6° C. Size of eye index at the starting time is plotted against the corresponding rate of increase of the eye index up to the time of hatching.

TABLE 1.—Lobster number, carapace length of female, age of eggs 10 January, increase of eye index of embryos from 10 January to 26 March, and the total developmental time for the embryos of the five female lobsters held under seasonal water conditions at the Boothbay Harbor Laboratory.

Lobster number	Carapace length (mm)	Area of capture	Age of eggs 10 January (weeks)	Increase of eye index (microns/week) 10 Jan.-26 Mar.	Total weeks to hatching
1	97	Boothbay Harbor	29	0.00	51.4
2	94	Boothbay Harbor	26	0.46	50.6
3	147	Veatch Canyon	24	0.65	50.0
4	124	Hudson Canyon	23	1.49	49.4
5	94	Boothbay Harbor	22	2.52	47.0

ure 2(A) the rate of eye increase (microns per week) of the embryos in each egg mass for the remainder of the developmental period is plotted against the corresponding eye index taken on November 7. The same result is obtained if the age of an egg mass is substituted for its eye index on the abscissa. Rates of increase were calculated by dividing the total increase of the eye index by the total number of weeks the embryos took to complete development after November 7. The increase in eye index (microns per week) of embryos in each egg mass, for the period January 10 to March 26, is presented in Table 1. During this time the water temperature ranged between 0.1° and 1.5° C; the mean was 1.0°. This was the coldest 10-week interval of the developmental period. The embryos in the oldest egg mass exhibited no noticeable or measurable increase in development during this time, whereas some development was noted in the embryos of the other egg masses. In fact, the embryos in the oldest egg mass showed no measurable increase from the second week of December to the middle of the following April. The number of weeks during the winter in which no development could be measured, for each egg mass, was as follows (as in Table 1, lobsters are numbered according to the age of their egg mass):

Lobster number	*Number of "dormant" weeks during winter*
1	18
2	14
3	8
4	6
5	0

The rates of increase (microns per week) in eye index for the embryos of seven lobsters held at a constant temperature of 22.6° C are indicated in Figure 2(B). These females came from offshore canyons of the continental shelf, off New England. The ages of these egg masses were not known, but the eye index of the embryos in each was measured before the females were placed in the warm water. The increase in eye index of the embryos in each egg mass was monitored weekly until hatching. Times and rates pertain only to the time spent at 22.6° C. Although one might expect that in a given time interval, at the same temperatures, younger embryos would develop faster than older ones, it might also be expected that the younger embryos would assume the slower growth rate of the older when they eventually reached the same age. Of

the five females held in water of seasonal temperature, the youngest eggs were at lower temperatures than the older at the same age, making assessment of differential developmental rate difficult. However, of the seven egg masses held at 22.6° C the embryos of least development at the start developed faster at comparable levels of development than the more advanced embryos. The differential rate of development of lobster embryos, at the same temperature, seems to imply that in a given population where extrusion of eggs may be somewhat staggered in time among the females, hatching of the eggs would occur during a more limited period, providing the egg-bearing females occupied the same thermal environment.

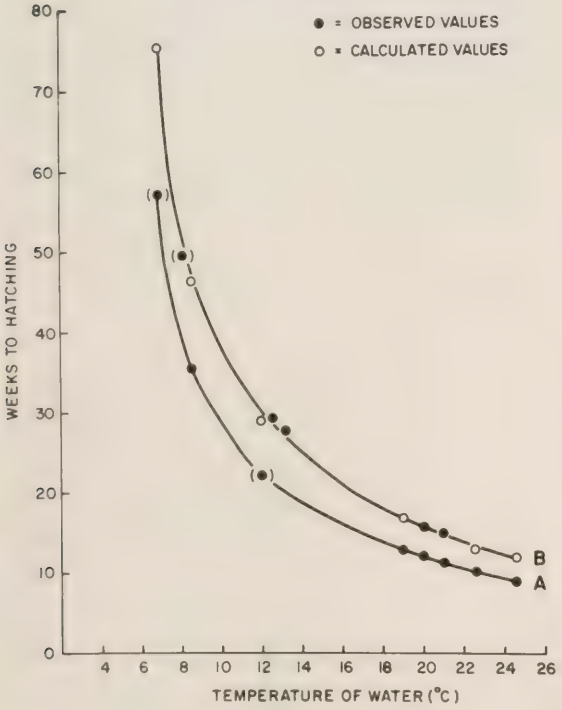

FIGURE 3.—The number of weeks for lobster eggs to complete the embryonic period at various temperatures. Line A represents the time required from onset of eye pigment in the embryos; line B represents the time required from extrusion to hatching. Points in parentheses indicate times required at the mean temperature of a fluctuating thermal environment.

RATES OF DEVELOPMENT AT VARIOUS TEMPERATURES

The times required for the embryos to hatch at various temperatures are shown in Figure 3. Line A represents the time required for the embryos to hatch after the formation of eye pigment; line B represents the time required from extrusion to hatching. Most of the points in each line indicate the time required to complete development at constant temperatures. A few (points in parentheses), representing the time required for total development at the mean temperature of a fluctuating thermal environment, have been included as well. For example, the average time required for total development of the eggs of the five females held under seasonal conditions was 49.7 weeks. The mean water temperature during the period was 8.1° C. These values are virtually the same as would be expected if the water was held constantly at 8° C.

All values showing time from onset of eye pigment to hatching were observed. The times required from extrusion to hatching at five temperatures were also observed. To find the unknown time required from extrusion to hatching, at other temperatures, I used the following equation:

$$\frac{A_1}{X_1} = \frac{A_2}{X_2}$$

where A_1 was the observed time from onset of eye pigment to hatching at 20° C; A_2 was the observed time from extrusion to hatching at 20° C; X_1 was the observed time required from

TABLE 2.—Number of weeks required from extrusion to onset of eye pigment, onset of eye pigment to hatching, and to hatching at certain temperatures, at salinities near 31‰.

Water temperature (° C)	Weeks required from		
	Extrusion to onset of eye pigment	Onset of eye pigment to hatching	Extrusion to hatching
5	40	120	160
10	9	30	39
15	5	18	23
20	4	12	16
25	3	9	12

onset of eye pigment to hatching at a given temperature; and X_2 is the unknown time required from extrusion to hatching at the same temperature as X_1. Templeman (1940, p. 74) used a similar method to find unknown developmental rates. The requisite times for development of lobster embryos at certain temperatures are summarized in Table 2. The relationship between water temperature and the average increase in eye index of lobster embryos, in microns per week, is linear at temperatures between 5° and 25° C. The index of the embryonic eye must increase to approximately 560μ at hatching. If eggs are encountered with eyed embryos, their eye index may be subtracted from 560 and the difference divided by the value calculated from the following equation:

$$\hat{Y} = -8.3151 + 2.6019(X)$$

where Y is the increase of the eye index in microns per week, and X is the developmental temperature. The resulting quotient is the average number of remaining weeks required for the embryos to hatch, depending on genetic variation and the differential rate of development noted earlier.

SUMMARY

1. Once eye pigment has been formed, the course and rate of development of lobster embryos may be monitored by the periodic measuring of the eye of the embryos.

2. Lobster embryos develop differentially, under the same thermal conditions, depending on their age or extent of development when they are subjected to a given thermal environment.

3. As water temperature has a direct effect on the developmental rate of lobster embryos, that rate may be manipulated by adjusting the water temperature of holding tanks to insure periodic hatches of larvae throughout the year.

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PRELIMINARY STUDIES OF SELECTED ENVIRONMENTAL AND NUTRITIONAL REQUIREMENTS FOR THE CULTURE OF PENAEID SHRIMP[1]

LOWELL V. SICK, JAMES W. ANDREWS, AND DAVID B. WHITE[2]

ABSTRACT

Types of substrate, type of aeration, and stocking density were compared as prerequisities for high-density culture studies with penaeid shrimps. Neither sand-shell substrate nor brick subdivisions of culture tank bottoms produced significantly higher survival rates than bare fiber glass tanks. Forced air supplied via airstones proved to be a more suitable form of aeration than did physical agitation of the water column in culture tanks by high-pressure nozzles. Survival rates of 80 to 90% were achieved when biomass densities did not exceed 40 g/m^2.

Semipurified pelleted diets (i.e., containing defined chemical ingredients plus one or more natural products) having a complement of nutrients including minerals and vitamins, various ratios of shrimp to fish meal, protein hydrolysates, and such diets fed at three percentages of total biomass daily were compared for their ability to produce increases in growth. Diets without fish or shrimp meal sustained biomass while those diets having the highest proportion of shrimp to fish meal in addition to added vitamins produced over 60% increase in total biomass over a 3-month period. Animals fed a combination of yeast, soy, and casein hydrolysates increased 39% in biomass over the same period of time while those fed each of the above hydrolysates during the 3-month period separately showed only an average of 18% increase in weight. Feeding shrimp with a fish-shrimp base with added vitamins at a rate of 15% daily of the total biomass produced a 164% increase in weight with 95 to 100% survival during the 3-month period. Using semipurified pelleted diets, a food conversion ratio of 5.5 was obtained.

Establishing selected preliminary environmental and nutritional requirements for penaeid shrimp resulted in the successful and reproducible production of major biomass increases with relatively high survival rates and low food conversion ratios.

The harvest of commercial shrimp suffers great seasonal variability and has failed to keep pace with ever-increasing domestic and export demands (Surdi and Whitaker, 1971). In order to supplement the natural harvest and provide a year-round supply of shrimp, several attempts have been made to culture shrimp in natural ponds, restricted portions of bays and estuaries, and laboratory tanks. In general, these efforts have had limited success and have explicitly illustrated the need for more accurately defining the nutritional and environmental requirements necessary for culturing these species. Although pond culture has produced annual crops of shrimps (Villadolid and Villaluz, 1951; Lunz, 1967; Wheeler, 1967; Broom, 1969; Moore and Elan, 1970[3]), production has been minimal and highly variable. Attempts to obtain commercial quantities of shrimp by stocking enclosed portions of estuaries have to date not yielded production results (American Fish Farmer & World Aquaculture News, 1970). During recent laboratory studies, Subrahmanyam and Oppenheimer (1969) were able to maintain shrimp in laboratory tanks using a pelleted diet consisting of fish meal, stickwater, and vitamins. However, the

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[3] Moore, W. R., and L. L. Elan. 1970. Salt water pond research. Tex. Parks Wildl. Dep., Austin. (Processed.)

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total biomass increase of shrimp fed their best diet for 6 weeks was only approximately 50% higher than initial biomass. Better results (on an individual weight basis) using *Penaeus duorarum* were obtained from animals grown on a sand substrate than those grown in bare tanks.

The greatest promise for economical shrimp production lies in determining the exact nutritional requirements and developing an inexpensive artificial diet from feedstuffs for these species. Current commercial practices in Japan employ chopped clam (predominantly *Tapes semidecussata*, Reeve) as a diet for rearing shrimp. Despite the high market price for cultured shrimp in Japan (the retail price of cultured shrimp ranged from $4 to $10 per pound in 1970), shrimp farming there tends to be a marginal enterprise because of the high cost of a clam diet. However, in other parts of the world where shrimp does not command such a luxury price, the use of a high-value product such as clam for shrimp feed is prohibited.

Pelleted diets (i.e., pellets containing all the chemical ingredients thought to be important to animal growth) have been designed consisting of purified soybean meal, glucose, sucrose, starch, glucosamine, chitin, cellulose, soybean oil, citric acid, succinic acid, amino acid, minerals, vitamins, and cholesterol (Kanazawa et al., 1970). After growing penaeids on such diets, the animals were in excellent physiological condition, but in the best group, total biomass increase was only 72% of the control group fed chopped clam. Thus, little progress has been made toward establishing nutritional and environmental requirements that will yield optimum growth (total biomass increase) and survival of penaeid shrimp.

In the present study, an attempt was made to develop a suitable experimental culture system which could serve as a model for future nutritional and environmental studies. Several environmental factors were examined, and, as a result, environmental conditions were created which would allow acceptable growth and survival. Having first established suitable culture conditions, several diets were evaluated in preliminary studies of the nutritional requirements of shrimp.

MATERIALS AND METHODS

Both environmental and nutritional studies were conducted in round fiber glass culture tanks measuring approximately 1 m deep by 1 m in diameter and equipped with a venturi type center drain which maintained a water depth of 0.75 m. Three replicates were maintained for all treatments.

Water (ranging in salinity from 26.8 to 29.3‰) from the Skidaway River was filtered through an oyster shell and sand filter to remove major food particles. Filtered water was heated to 30° C in a stainless steel heat exchanger and jetted into each tank at a rate of 1.9 liters/min through flow-control nozzles which were aimed so that the agitation of the water column in each tank was minimal. Temperature ranged from 25° to 28°C in each tank throughout the experimental period.

White shrimp (*P. setiferus*) obtained from the Savannah, Ga., river and tributary systems were used in all environmental experiments, and brown shrimp (*P. aztecus*) obtained from the Tampa Bay, Fla., area were used in the nutritional studies. Shrimp weighing 4 ± 0.8 g (mean and standard deviation based on 480 weighed shrimp) were selected from the above stock and used in all environmental studies (10 animals per tank) and fed pelleted diets (Table 1, Diet 1) at a rate of 5% of their biomass daily, on a dry weight basis. Shrimp were weighed each week and the percent increase or loss recorded on a wet weight basis.

SUBSTRATE STUDY

Sand-shell substrates suitable for burrowing, subdivisions of tank bottoms, and bare fiber glass tank bottoms were provided for replicate groups of shrimp, and relative survival rates among the treatment groups were compared over a 5-week period. Sand-shell substrates were placed directly onto the tank bottom in one group, and in another group, the same substrate was placed on a perforated platform 10 cm above the tank bottom, allowing a flow of water through the drain below the sand surface. Such an arrangement was designed to test the effect of decreasing the

TABLE 1.—Experimental variables and results from four nutritional studies with penaeid shrimp.

	Group I, Diets				Group II, Diets					Group III, Diets					Group IV, Diets			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Casein (%)	50.2	50.2	50.2	--	28.5	8.0	28.5	23.5	--	--	--	--	--	--	8.0	8.0	8.0	--
Methionine (%)	1.0	1.0	1.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Glycine (%)	0.1	0.1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Sodium glutamate (%)	0.2	0.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Citric acid (%)	0.3	0.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Succinic acid (%)	0.3	0.3	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Mineral mix[1] (%)	5.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Fat[2] (%)	8.0	8.0	8.0	--	8.0	8.0	--	8.0	--	8.0	8.0	8.0	8.0	--	8.0	8.0	8.0	--
Carbohydrate premix[3] (%)	20.5	20.5	20.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Shrimp meal (%)	--	--	--	--	28.5	69.5	36.5	23.5	--	28.5	28.5	28.5	28.5	--	69.5	69.5	69.5	--
Anchovy meal (%)	--	--	--	--	28.5	8.0	28.5	23.5	--	28.5	28.5	28.5	28.5	--	8.0	8.0	8.0	--
Shrimp muscle (%)	--	--	--	--	--	--	--	15.0	--	--	--	--	--	--	--	--	--	--
Yeast protein hydrolysate[4] (%)	--	--	--	--	--	--	--	--	--	24.5	--	--	8.1	--	--	--	--	--
Casein protein hydrolysate[4] (%)	--	--	--	--	--	--	--	--	--	--	24.5	--	8.1	--	--	--	--	--
Soy protein hydroysate[4] (%)	--	--	--	--	--	--	--	--	--	--	--	24.5	8.1	--	--	--	--	--
Collagen (%)	4.0	4.0	4.0	--	4.0	4.0	4.0	10.0	--	8.0	8.0	8.0	8.0	--	4.0	4.0	4.0	--
Vitamin mix[5] (%)	2.5	2.5	2.5	--	2.5	2.5	2.5	2.5	--	2.5	2.5	2.5	2.5	--	2.5	2.5	2.5	--
Cellulose (%)	7.9	12.9	13.8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Daily feeding rate (% of biomass)	5	5	5	0	5	5	5	5	0	5	5	5	5	0	5	10	15	0
Duration (weeks)	5	11	11	11	11	11	11	11	11	6	6	6	6	6	6	6	6	6
Results:																		
% increase in biomass	18	0	0	0	44	63	50	37	--	19	18	18	39	--	58	109	164	--
Survival rate (%)	80	80	80	0	90	100	90	80	0	90	80	80	90	27	80	90	90	26

[1] Contains 30.0% K_2HPO_4, 9.4% KCl, 14.8% $MgSO_4$, 27.4% $CaHPO_4 \cdot 2H_2O$, 1.4% $FeCl_3$, 0.2% $MnSO_4 \cdot 7H_2O$, and 16.8% $CaCO_3$.
[2] Contains 33⅓% corn oil, 33⅓% hydrolyzed vegetable and animal fat, and 33⅓% menhaden oil.
[3] Contains 24.3% corn starch, 24.3% sucrose, 24.3% glucose, 19.5% chitin, and 7.6% glucosamine.
[4] Nutritional Biochemical Co. enzymatic hydrolysates.
[5] Nutritional Biochemical Co., Cleveland, Ohio, standard vitamin diet fortification mixture in dextrose.

buildup of anaerobic conditions. Division of tank bottoms into sundry tunnels and levels was created by specific placement of bricks and clay drain tiles.

AERATION STUDY

Aeration provided by jetting streams of filtered seawater into respective tanks was compared to aeration supplied by bubbling air through airstones into tanks in which water was continuously added with no agitation of the water column for an 8-week period. Two airstones were placed in each tank and valve-regulated air lines controlled the pressure at approximately 4 psi. Oxygen levels were monitored periodically and used along with survival rates as a basis for evaluation of replicate groups aerated by each method.

STOCKING DENSITY STUDY

Survival data were compared among triplicate tanks stocked at 10, 20, and 40 shrimp per m^2 for an 8-week period. These densities of approximately 40, 80, and 160 g/m^2 were chosen on the basis of data provided in pond and laboratory culture of penaeid shrimp (Broom, 1969; Subrahmanyam and Oppenheimer, 1969).

PRELIMINARY NUTRITIONAL STUDY

Triplicate groups of ten 4 g brown shrimp (*P. aztecus*) were fed a series of pelleted diets. Growth data (biomass increase) was used as a means of evaluation. Diets examined consisted of those patterned after Japanese purified diets (i.e., diets containing only chemical ingredients) (Table 1, Group I) (Diet 1 was conducted for 5 weeks and Diets 2, 3, and 4 for 11 weeks each); a second group of semipurified diets (i.e., containing defined chemical ingredients but containing one or more natural products) providing four combinations of levels of protein, fat, shrimp, and fish meal (Group II) (conducted for 11 weeks); and a third group designed to compare the nutritional value of casein, yeast, and soy hydrolysates (Group III) (conducted for 6 weeks). All of these groups were fed at 5% of their respective biomass daily. In addition, Diet 6 was fed at 5, 10, and 15% of biomass (Group IV) (conducted for 6 weeks).

TABLE 2.—Percent of pellet dissolved over time and at at three concentrations of binder. (Values are means and standard deviation on two replicates with Diet 1.)

Percent binder (collagen) added	Hours		
	6	12	24
1			
3	13 ± 1.2	14 ± 0.9	18 ± 1.7
5	11 ± 0.8	10 ± 0.6	10 ± 0.6
10	10 ± 0.6	10 ± 1.1	10 ± 1.0

Combined environmental factors which produced best survival in each of the environmental experiments (i.e., culture conditions consisting of bare fiber glass tank bottoms, supplied aeration, and a stocking density of approximately 40 g/m^2) were used in all nutritional studies. This combination offered a maximum potential for an increase in biomass and therefore allowed accurate evaluation of differences among diets tested. Although survival in bare fiber glass tanks was not significantly different from sand substrates, the fact that bare tanks were simpler to maintain dictated that they be used for the nutritional studies.

Prior to starting nutritional studies, the physical properties of pelleted diets were evaluated for acceptability as shrimp food. Pellet consistency was determined according to its ability to resist dissolution over a given period of time, and texture and size were chosen according to animal performance when presented several choices. Collagen[4] proved to be a suitable binding agent. Using an experimental design with time and collagen levels as variables, a pellet with 5% collagen added as a binder was found to offer optimum consistency over a 24-hr immersion in salt water (Table 2). Percent dissolution was measured by taking dry weights after 6, 12, and 24 hr of immersion (no shattering of pellets was observed, and all loss of weight was therefore assumed to be from dissolution). Animals were observed to feed most readily on

[4] Supplied on an experimental basis by the Hides and Leather Division of the U.S. Department of Agriculture Eastern Utilization Laboratory in Philadelphia, Pa.

pellets 0.3 cm in diameter by approximately 1.5 cm in length and which sink in water, and hence, pellets having these characteristics were used in both environmental and nutritional experiments.

RESULTS AND DISCUSSION

SUBSTRATE STUDY

A survival rate of 80% was obtained after 5 weeks in tanks without substrate, 80 to 90% survival was maintained over much of the duration of the experiment among both treatments having sand-shell substrates, and less than 60% survival occurred among tanks having brick subdivisions (Figure 1). Although *P. setiferus* is reported to burrow less than either *P. duorarum* or *P. aztecus* (Anderson, 1966; Pérez Farfante, 1969), it apparently was able to avoid predation, especially during the highly vulnerable moulting period, quite successfully with or without a sand substrate, since 5-week survival data among the two sand-shell treatments and the bare tank bottom treatment were not significantly different ($P < 0.05$) (Duncan, 1955). If the type of shelter is a factor in increased survival for penaeids maintained under culture conditions, the brick subdivisions should have enhanced survival. However, the markedly high mortality rate among this group, significantly different from the other three treatments ($P < 0.05$), may have resulted from either failure of the shrimp to behaviorally segregate and thus fully utilize this protection or from physical abrasion against the sharp and coarse brick surface. Although there may have been toxic substances in the brick materials, the bricks were carefully washed and assumed to be otherwise inert in any chemical effect they may have had on the animals. Although differences in volume of water caused by placing various substrates in their respective treatments was not controlled for, it was felt that these differences in a running water system were not critical to the survival of shrimp. Differences in bottom area among the treatments caused by placement of different types of substrate were neither controlled for nor measured but were also thought to be negligible compared to differences found among treatment groups. The high degree of cannibalism noted by Subrahmanyam and Oppenheimer (1969) in tanks without substrate was not observed in any groups.

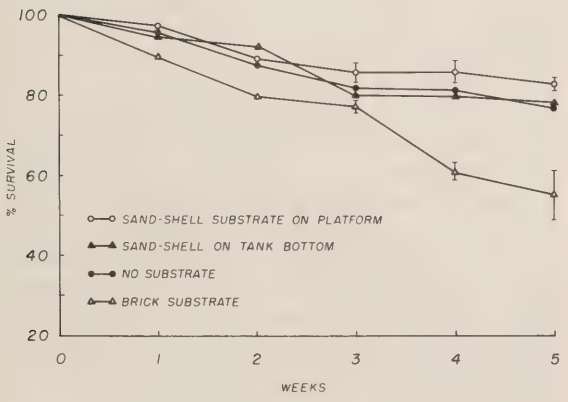

FIGURE 1.—Mean and standard error for percentage of animals surviving after 5 weeks of growth on four different substrates.

AERATION STUDY

The group having oxygen supplied by injecting air through airstones had significantly higher survival rates ($P < 0.05$) when compared with a treatment aerated by agitation of the water column (Figure 2). Although the average oxygen levels were similar between the two treatments (3.4-6.8 ppm), such levels in tanks aerated by high-pressure nozzles often dropped for short intervals due to clogging of the nozzles with silt and biological debris. Electrical power failures which affected water flow but not the compressed air supply (equipped with stand-by DC power) also caused intermittent drops in oxygen levels. Such short-term irregularities may have been more critical to shrimp tolerances than is indicated from reference to average oxygen level values, per se. Also, at the relatively high temperatures maintained throughout the study, short drops in oxygen levels could have been very critical. Decreased survival in tanks with agitation of the 0.75-m water column may also have resulted from physical agitation of the animals.

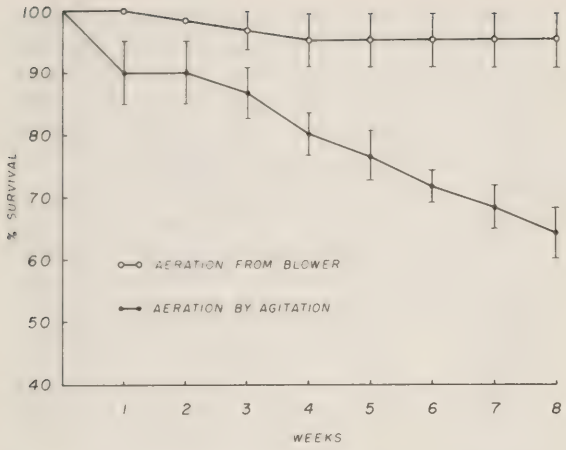

FIGURE 2.—Mean and standard error for percentage of animals surviving after 8 weeks of growth with two types of aeration.

STOCKING DENSITY STUDY

Stocking densities higher than 40 g/m² produced proportionally higher mortalities indicating an approximate carrying capacity for this particular culture system (Figure 3). If shrimp were stocked at 40 g/m², a population of 32 g/m² remained after 8 weeks. Similarly, when shrimp were stocked at 80 g/m², a relatively stable population of approximately 52 g/m² existed during the final 2 weeks of study. Similarly, mortality during the first 8 weeks among a population originally stocked at 160 g/m² created a population of approximately 80 g/m², but in this case the survival rate was still declining after 8 weeks of growth. Therefore, a carrying capacity (maximum biomass obtainable) for this culture system may have been somewhere between 32 and 80 g/m².

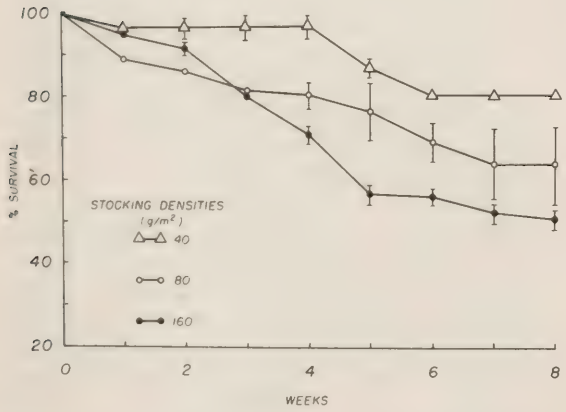

FIGURE 3.—Mean and standard error for percentage of animals surviving after 8 weeks of growth at three stocking densities.

Although such a carrying capacity would depend on the particular culture system, applicable calculations, utilizing data from a laboratory culture study (Subrahmanyam and Oppenheimer, 1969) and a pond culture experiment (Broom, 1969), indicate a similar carrying capacity for populations of other systems (ponds, embayments, and laboratory tanks). In the case of the laboratory study, best survival was obtained when shrimp were stocked initially at 34 g/m², yielding a biomass of 27 g/m² at the termination of the experiment. Likewise, best survival and an increase in biomass occurred in the pond culture study when initial stocking densities were below 20 to 30 g/m². Recent data from a commercial operator in Central America indicates that, regardless of stocked biomass, the carrying capacity ranged from 5.5 to 7.3 g/m² (Smitherman and Moss, 1970). Such evidence suggested that final production expectations should be considered in choosing initial stocking densities.

PRELIMINARY NUTRITIONAL EXPERIMENTS

A comparison of several groups of diets (Table 1) revealed that semipurified diets with casein as the major source of protein (Group I), only produced an average of 18% increase in biomass above stocked biomass levels. Group II, having fish and shrimp meal as additional sources of protein, produced approximately 63% growth on the best diet. Group III diets comparing hydrolyzed proteins yielded only 39% growth on the best diet, and animals fed at a rate of 15% of their total biomass (Group IV) increased their initial biomass 164%. In addition to increased

growth above that obtained in the environmental studies, survival was increased from 80 to 90% to 90 to 100% through the information acquired from the above nutritional comparisons.

Shrimp obtained little if any sustenance from organic or settled detritus since the continuous flow of filtered seawater through the tanks kept the system relatively free of siltation and extraneous growth. Furthermore, starved animals were not able to sustain their initial biomass level beyond 2 weeks, and the populations in all three replicate tanks had died after 7 weeks. Cannibalism appeared to be prevalent among starved organisms, and the decline in weight was undoubtedly moderated due to growth of animals preying upon dead shrimp.

Diets in Group I with casein as the major protein source produced little growth above sustenance. Diet 1 with an added mineral mix yielded a significantly higher biomass increase above initial weights at the 5% feeding level than either Diets 2 or 3 which lacked the mix. In addition to the mineral mix, Diet 3 lacked sodium glutamate, glycine, citric acid, and succinic acid and correspondingly caused a loss in biomass over the 3-month growth period. Although the above results showed Diet 1 to be significantly different ($P < 0.05$) from the other diets after the first month of study, results are somewhat confounded with initial differences in stocked biomasses and poor response in general.

These sustenance biomass levels represented far less growth increase than the 72% of control obtained by Kanazawa et al. (1970) and may be due to a lack of cholesterol in our study. Since many crustaceans are not able to synthesize cholesterol (Van Den Oord, 1964; Dall, 1965; Zandee, 1967), including recent evidence for shrimp (Kanazawa et al., 1971), the lack of this entity undoubtedly was attributed to the poor performance of these diets.

Shrimp fed on Group II diets averaged a 37 to 63% increase in growth. Although results from Diets 5, 6, and 7 were not significantly different ($P < 0.05$), Diet 6, which consisted of a high ratio of shrimp to fish meal and a low level of casein, yielded greatest biomass increases. Total biomass decreased in diets having a decrease in percentage of shrimp meal. Growth from Diet 8, which contained blended shrimp muscle and lower levels of shrimp and fish meal, was statistically less ($P < 0.05$) than the other three diets. Again, the control group of starved shrimp was not able to sustain its initial weight and declined in biomass after the first 2 weeks.

Group III, consisting of yeast, casein, and soy protein hydrolysate diets, produced an average biomass increase of 18 to 39% (Table 1). The combination of diets containing casein, soy, and yeast hydrolysates produced significantly better ($P < 0.05$) growth than individual hydrolysates. Since results from this group were not better than results after 6 weeks from Diet 5 which was similar except it contained only intact protein, these data indicate that hydrolyzed proteins are not utilized more efficiently than intact proteins.

Comparing food supplied at 0, 5, 10, and 15% of total biomass using Diet 6 illustrated that growth was directly proportional to an increase in feeding rate (Group IV), and may reflect the natural feeding habit of the species. While the population of starved animals disappeared after 8 weeks, the treatments fed at 5% of their biomass increased 58% over their initial weight; those fed at 10% of their biomass increased 109%; and those fed at 15% biomass gained 164%. The above results indicate that penaeids are capable of consuming large amounts of food. This may be a reflection of their natural tendency to continuously graze upon large quantities of benthic material rather than feed periodically as would a strict carnivore. Although pellets used in all experiments were textured to maintain consistency in solution for 24 hr, some shattering may occur as shrimp gnaw at them and thus some food may be lost through flushing, thus decreasing the efficiency of ingestion as feed levels are increased.

Although growth was directly proportional to an increase in feeding rate, feeding at low levels was still justified in attempting to determine nutritional requirements of shrimp. The benthic material normally grazed upon is low in energy content and is often of relatively poor nutritional content. Feeding at lower fed levels but with food of proper nutritional value could conceivably produce growth comparable to higher fed

levels of natural or formula diets presently known.

Food conversion ratios (FCR) (weight of food fed for 6 weeks/weight increase) were calculated from results in Group IV (calculated on a dry weight basis). Feeding at 10% biomass yielded an FCR of 6.7 and growth increase of 109%. On the other hand, feeding at the 15% level produced a 164% growth increase and an FCR of 5.5. Such FCR, although not comparable to those obtained for vertebrates such as the 1.6 or less for catfish (Andrews, in press), nonetheless represent a significant decrease over the FCR of 10 or greater reported for shrimp fed on natural foods (Fujinaga, 1963). Further refinement of the FCR for penaeids can undoubtedly be obtained through procurement of a more suitable pellet, better understanding of exact nutritional requirements of specific nutrients, and more information on ingestion and assimilation phenomena.

SUMMARY

1. Environmental conditions yielding 80 to 90% survival in the intensive tank culture of penaeid shrimp encompassed a combination of either no substrate or sand substrate on elevated platforms, air supplied externally by an aeration system, and population density of 40 g/m^2.

2. Diets having balanced complements of proteins, lipids, carbohydrates, amino acids, fatty acids, minerals, and vitamins produced only sustained biomass levels.

3. Diets having 69.5% of the total diet as shrimp meal produced growth increases of 63%.

4. Examination of soy, casein, and yeast hydrolysates revealed that a combination of each produced 39% growth increase while an average of 18% resulted from feeding each hydrolysate separately. Hydrolyzed proteins did not yield better growth than intact proteins.

5. Feeding at 5, 10, and 15% of the animals' biomass daily yielded directly proportional growth. A growth increase of 164% was achieved with a fish meal and shrimp meal diet fed at 15% of biomass daily.

6. Using semipurified pelleted diets, food conversion ratios were reduced by nearly half of that reported for penaeids feeding on clam and other natural foods.

7. Establishing selected preliminary environmental and nutritional requirements for penaeid shrimp resulted in reproducible production of major biomass increase with relatively high survival and low food conversion ratios.

8. Results from these studies have allowed us to design facilities and experiments for future work with environmental and nutritional factors. Development of an inexpensive diet which will yield rapid and maximum growth will be an essential requirement for economical production of penaeid shrimp.

ACKNOWLEDGMENTS

The authors wish to sincerely thank Lee H. Knight and his engineering crew for their night and day effort to establish and maintain the facilities and auxiliary power units that were essential for this study. In addition, we are grateful to Harry Carpenter and his crew for their efforts in general construction and maintenance of our mariculture facilities.

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METHOD OF DETERMINING CAROTENOID CONTENTS OF ALASKA PINK SHRIMP AND REPRESENTATIVE VALUES FOR SEVERAL SHRIMP PRODUCTS

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ABSTRACT

An extraction method is described for estimating the amount of carotenoids in pink shrimp. The carotenoid index is useful as a measure of quality and as an indicator of changes during storage. Values for several shrimp products are reported.

The carotenoid content of Alaska pink shrimp is affected by many conditions and can be used as an index of the general quality of canned shrimp and of the changes in quality of frozen shrimp during storage. It has been also used as a factor in determining optimum peeling characteristics of shrimp (Collins and Kelley, 1969) and in selecting desirable retorting conditions (Kelley, 1971[3]). Color differences in shrimp at different seasons and in different areas may be important in harvesting and marketing practices.

The carotenoid in Alaska pink shrimp is primarily astaxanthin. Both total astaxanthin and astacin, its oxidation product, are measured by the method to be described, which was developed for use with frozen Alaska king crab (Ravesi, 1965[4]) and adapted to Alaska pink shrimp which contain more interfering protein and moisture than crab.

METHOD OF DETERMINING CAROTENOID CONTENTS

To 50 g of blended meat add approximately 10 g of silica gel and 100 ml of the proper acetone solution:

1. 75% acetone for canned shrimp with liquor.
2. 65% acetone for frozen cooked or raw meats.
3. 50% acetone for raw shrimp with shells on.

The silica gel, which serves as a filter aid, is not essential but makes subsequent extraction and filtration easier. Blend just enough to ensure complete mixing and filter through a medium porosity fritted glass funnel, maintaining suction until dripping ceases. Rinse container and filter as needed with 50% acetone. Discard colorless filtrate and blend residue about 2 min with 15 to 20 g anhydrous sodium sulfate and 100 ml of 1:1 2-propanol:chloroform. Filter and re-extract with 50 ml solvent one or two times as needed to get a colorless meat. Use 2-propanol:chloroform as rinse solution during these extractions. Transfer filtrate to 500 ml round bottom flask and strip the solvent, using a rotating vacuum evaporator. Add 5 to 10 ml chloroform and evaporate to dryness. Dissolve residue in enough pure cyclohexane to wash sides of flask and add 10 to 15 g anhydrous sodium sulfate. Let set for a few minutes and filter through sodium sulfate on a fine porosity fritted

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glass funnel, washing sodium sulfate with cyclohexane to remove all traces of color. If filtrate is clear, dilute to 100 ml. If it appears hazy, repeat the filtration, allowing solution to remain in fresh sodium sulfate for a brief time. Read at 474 nm on spectrophotometer, using cyclohexane as a blank.

The precision of the method was determined by analyzing 11 identical samples in quadruplicate on 11 different days. Twenty-two cans of the same code of canned shrimp were blended in a Waring blendor, and the homogeneous mixture was sealed in cans and frozen at —60° F. For each day's sampling, two cans of the frozen mixture were thawed and blended together.

Different lots of solvents were used at intervals to determine the sensitivity to slight variations in solvents. The solvent lot was not critical but the cyclohexane used in the spectrophotometer should be carefully distilled within a few days of use. We used a Gilford modification of a Beckman DU spectrophotometer[5] which gives readings with three place accuracy. The range of absorbance readings was 0.420 to 0.452, the average was 0.436, and the standard deviation was 0.008.

The carotenoid content, expressed as the carotenoid index, is a calculated value based on dry weight. The solids content of the shrimp was determined by the Association of Official Agricultural Chemists method (Horwitz, 1965: 346), using 5 to 10 g of the blended meat sample and heating at 105° C for 18 to 24 hr. The carotenoid index represents the absorbance (A) in 100 ml of solvent of the carotenoids from 1 g of dry sample, measured in a 1-cm cell. It is calculated as follows:

$$C_I = \frac{(\text{A at 474 nm in 100 ml cyclohexane})\,(100)}{(\text{50-g wet sample})\,(\%\ \text{dry weight})}$$

The absorbance reading of a shrimp sample with average moisture content is roughly 10 times larger than the carotenoid index; therefore the carotenoid index equivalent of the standard deviation is slightly less than 0.001.

[5] The use of trade names is merely to facilitate description and does not imply endorsement of a product.

The amount of carotenoid can also be expressed as grams of pigment/gram tissue by using the extinction coefficient of 2150, as reported by Kanemitsu and Aoe (1958). The amount of astacin present in fresh shrimp is small and since the extinction coefficients of astacin and astaxanthin for calculation purposes do not introduce significant error for routine analytical work, the calculation would be:

$$\text{grams pigment/1 g tissue} = \frac{(A \text{ at } 474 \text{ nm})\,(100 \text{ ml})}{100\ (50\text{ g})\ (d)\ (2150)}$$

where d is the cell width in centimeters. This could be converted to dry tissue weight by multiplying by the percent of solids in the sample.

CAROTENOID CONTENTS OF VARIOUS TYPES OF SHRIMP SAMPLES

Table 1 gives carotenoid values of various types of shrimp samples described. Most of the data were collected as part of some other project so these samples are from several lots of shrimp caught at different times of the year. Only those grouped together in the table can be accurately compared with each other. All data, however, represent an average figure for the given sample and may be used to compare types of sample products or processing methods.

TABLE 1.—Carotenoid values for 11 shrimp samples.

	Sampling conditions	Carotenoid index	Cause of color differences indicated by data
1.	Raw tails, shells on	0.237	
	Raw meats	0.086	
2.	Whole cooked, hand-peeled meats, frozen	0.112	
3.	Precooked, machine-peeled meats, frozen	0.086	
	After 6 months' storage	0.070	Storage time
	After 12 months' storage	0.062	
4.	Precooked, machine-peeled canned	0.073	Precook versus ice held conditioning
	2-day iced, machine-peeled, canned	0.059	
5.	1-day not iced, precooked, machine-peeled, canned	0.080	
	2-day iced, precooked, machine-peeled, canned	0.066	Time of ice holding
	3-day iced, precooked, machine-peeled, canned	0.064	

EXPERIMENTAL PROCEDURE

1. The shrimp were frozen whole as soon as possible after being caught, then were shipped to the laboratory. They were partially thawed, weighed, and separated according to weights. The shrimp used were about 80 count. All were headed and some were hand peeled to obtain meats. The tails with shells on and the peeled meats were refrozen as needed until analyses could be made.

2. Whole cooked, hand-peeled frozen shrimp meats were obtained from a commercial processor. This is the conventional, cocktail style product.

3. Precooked, machine-peeled shrimp were produced under experimental conditions in a commercial plant. Shrimp were landed within 24 hr of catching, held overnight without ice, and precooked at 165° F for 10 sec, 110° F for 2 min, and machine peeled. The meats were collected at the end of the inspection belt and frozen in cans without vacuum. Analyses were made within a few days, after 6 months, and after 12 months of 0° F storage.

4. Precooked, machine-peeled canned shrimp were produced as described above except they were routinely retorted. The 2-day iced, machine-peeled shrimp are a standard commercial pack from the same lot of shrimp.

5. The 1-day not iced; 2-day iced; and 3-day iced, precooked machine-peeled, canned shrimp were also experimentally produced in a commercial plant. The 1-day not iced shrimp were held in the wooden boxes in which they were landed. The 2- and 3-day iced shrimp were held in large tanks and ice added as needed to keep them cool. All of these shrimp were precooked at 165° F for 10 sec, 110° F for 2 min, and then routinely peeled and canned.

All samples were analyzed using the previously described method of determining carotenoid contents. The averages reported in Table 1 represent 3 to 12 determinations under the given sampling conditions.

Some of the factors which cause differences in the carotenoid content of shrimp are shown in Table 1. These include several processing variations which can be controlled by processors and fishermen.

CONCLUSIONS

The method of determining carotenoid content described is simple and precise and may be used on a variety of shrimp product forms.

The carotenoid index for Alaska pink shrimp varies from 0.267 in raw tails to 0.059 in ice held, machine-peeled canned shrimp. Correlation with subjective color rating is quite good (Collins and Kelley, 1969). At the higher color levels found in raw, hand-picked, or precooked shrimp, small differences are difficult to detect visually and the determination of the carotenoid index becomes even more useful in evaluating samples.

Since the carotenoid content is usually closely correlated with other quality characteristics, the carotenoid determination may be useful in making decisions about the best ways to process or handle shrimp.

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A DESCRIPTION OF YOUNG ATLANTIC MENHADEN, *Brevoortia tyrannus*, IN THE WHITE OAK RIVER ESTUARY, NORTH CAROLINA

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ABSTRACT

Atlantic menhaden exhibit three different stages—larva, prejuvenile, and juvenile—during their stay in the estuary. For specimens collected from the White Oak River estuary, N.C., the length-weight relation was $\log_e \hat{Y} = -8.1104 + 3.6050 (\log_e X)$ for larvae, $\log_e \hat{Y} = -16.9638 + 6.3083 (\log_e X)$ for prejuveniles, and $\log_e \hat{Y} = -5.2298 + 3.1452 (\log_e X)$ for juveniles, where Y = weight in mg and X = length in mm. Larvae and prejuveniles concentrated in the low salinity-freshwater zone upstream. Juveniles tended to move downstream toward the higher salinity water. Condition factors of larvae and prejuveniles increased toward the higher salinity zone.

Atlantic menhaden spawn and hatch in coastal oceanic waters from Maine to Florida. The larvae enter estuaries where they transform into juveniles near the freshwater zone. The relation of young menhaden length and weight to time, salinity, and location within an estuary provides insight on the environmental requirements of menhaden during a critical phase in their life cycle. We collected young menhaden from a small estuary in North Carolina, from March to September 1969 with a tidal net (Lewis et al., 1970) to study changes in the length-weight relation.

The lower portion of the White Oak River estuary (28 sq km) is shallow with depths from 0 to 3.0 m and distances from opposing shores from 1 to 3 km. The intracoastal waterway crosses the lower estuary and is maintained at a depth of approximately 4 m. The upstream portion narrows into a river up to 4.6 m deep. During the study period we generally found that the change from brackish to fresh water occurred between 18 and 24 km upstream from Bogue Inlet. The exact location of this low salinity zone was influenced by tide, rainfall, and direction and speed of the wind. The mean tidal range at Bogue Inlet is 2.2 ft (0.67 m) (U.S. Coast and Geodetic Survey, 1970). At 21 km upstream the average river flow is 14.7 cfs (0.42 m^3/sec) (North Carolina State Board of Health, 1954). A map showing the location of the White Oak River estuary is shown in Lewis and Mann (1971).

We selected 14 stations from Bogue Inlet to 34 km upstream (Wilkens and Lewis, 1971). Stations ranged from 2 to 5 km apart and were selected to be representative of the various salinities encountered. We also sampled in fresh water to determine how far menhaden move upstream. Salinity measurements were taken within 1 m of the surface. During collections, spot checks of salinity between the surface and bottom indicated that in this shallow estuary thorough mixing generally occurred. Differences between measurements at one location were due to flooding and ebbing tides.

Our menhaden collections ranged from 15 to several thousand individuals. We measured and weighed all fish to the nearest 0.5 mm total length and 0.1 mg in collections containing less than 26 and subsampled the larger collections. Since both length and weight variances in the subsamples were small, we considered our estimates of length and weight to be reliable. Our measurements of total length were based on the greatest dimension between the most anteriorly projecting part of the head and the farthest tip

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of the caudal fin when the caudal rays are squeezed together (Hubbs and Lagler, 1949).

We separated young menhaden into three stages on the basis of body form and the length-weight relation of individuals within each stage. Length and weight ranges of all the fish used in the study are given in Table 1. An illustration of each stage (larva, prejuvenile, and juvenile) that occurs during the first year in the estuary is shown in Figure 1.

Allometric growth, with stanzas for larvae, prejuveniles, and juveniles is shown in Figure 2. The inflection points, indicating change in slope, are 30 and 38 mm for length, and 70 and 469 mg for weight. We considered specimens less than 30 mm and 70 mg as larvae; they are long and slender, and even at 30 mm total length the body depth is only 4 mm or less. In the next group,

TABLE 1.—Lengths and weights of Atlantic menhaden from the White Oak River estuary, N.C., arranged in order of increasing weight classes.

Weight	Length range	Number of menhaden	Weight	Length range	Number of menhaden
mg	*mm*		*mg*	*mm*	
0.0- 4.9	8-16	23	100.0- 199.9	29-34	38
5.0- 9.9	14-20	46	200.0- 299.9	33-37	26
10.0-14.9	17-21	43	300.0- 399.9	35-38	6
15.0-19.9	20-23	48	400.0- 499.9	37-43	5
20.0-24.9	20-24	45	500.0- 599.9	39-41	10
25.0-29.9	22-26	32	600.0- 699.9	40-44	14
30.0-34.9	23-26	30	700.0- 799.9	41-44	11
35.0-39.9	24-27	31	800.0- 899.9	44-45	6
40.0-44.9	25-28	29	900.0- 999.9	45-49	4
45.0-49.9	25-29	10	1,000.0-1,499.9	47-54	41
50.0-54.9	26-29	20	1,500.0-1,999.9	53-60	27
55.0-59.9	27-29	26	2,000.0-2,499.9	58-62	16
60.0-64.9	27-31	26	2,500.0-2,999.9	61-66	11
65.0-69.9	27-31	19	3,000.0-3,499.9	68-71	5
70.0-74.9	28-31	22	3,500.0-3,999.9	71-74	8
75.0-79.9	29-32	15	4,000.0-4,499.9	75-77	4
80.0-84.9	29-32	12	4,500.0-4,999.9	76-82	5
85.0-89.9	29-31	7	5,000.0-5,499.9	81	3
90.0-94.9	28-32	11	5,500.0-5,999.9	81-83	2
95.0-99.9	29-32	6			

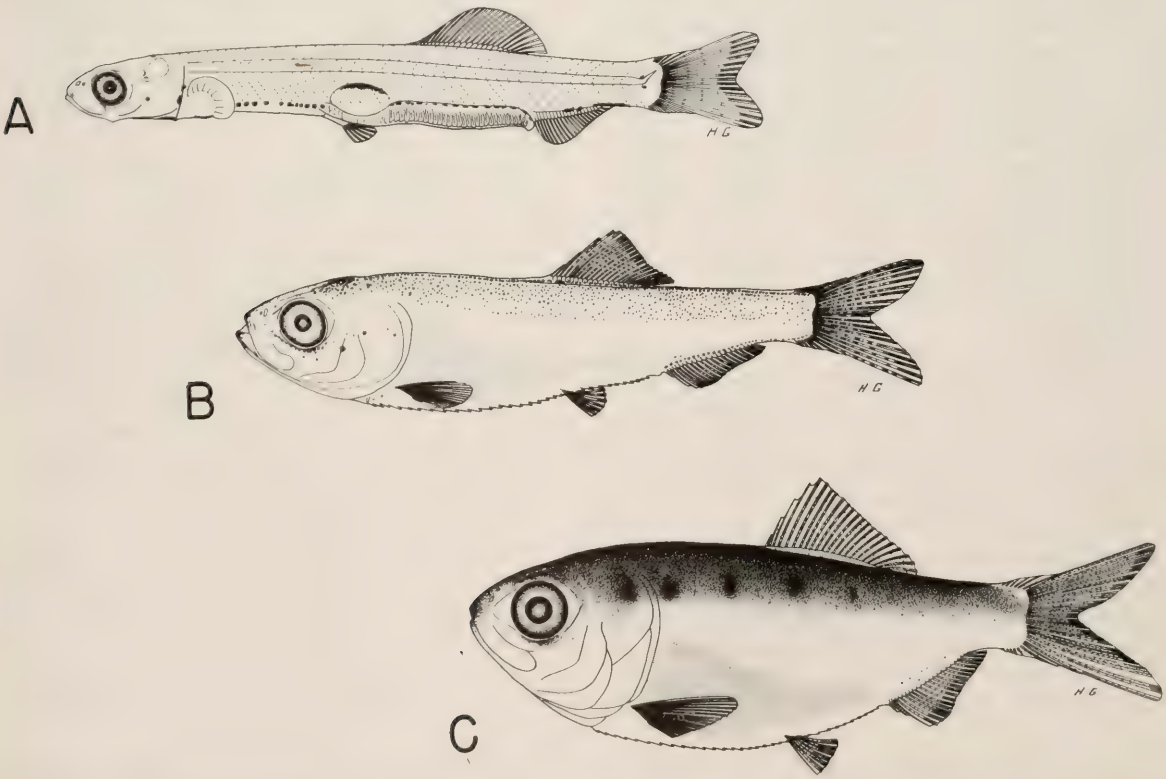

FIGURE 1.—Atlantic menhaden (a) larva 27.0 mm total length (TL); (b) prejuvenile 32.0 mm TL; and (c) juvenile, 64.0 mm TL. The alimentary tracts are shown as they were visible in the preserved specimens used in drawings.

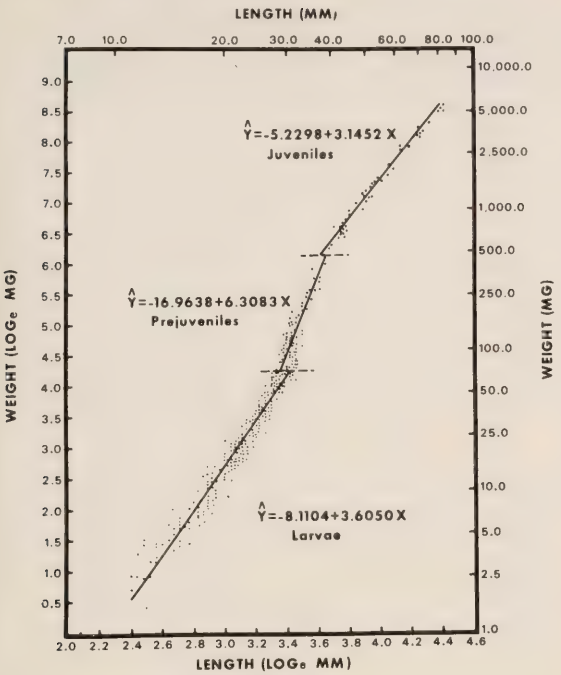

FIGURE 2.—Regression of weight on length for larval, prejuvenile, and juvenile Atlantic menhaden collected in White Oak River estuary, N.C., in 1969. (We separated the lengths and weights into three groups after visual observation of the data and fish. Lines were then fitted by least squares regression based on data in each group.)

prejuveniles, we included specimens from 30 to 38 mm and 70 to 469 mg. In this stage there is a rapid increase in body depth, but little increase in length. Fish above 38 mm and 469 mg we classed as juveniles. Huntsman[3] found that the relation between length and weight is similar for juveniles and adults. Both stages have a similar body form, only their color and size being different. We did not find any adults in our estuarine study.

Larvae enter the lower estuary and move upstream to the freshwater-low salinity zone where they go through a prejuvenile stage before completing their transformation into juveniles.

[3] Huntsman, Gene R. 1971. Growth by year class of Atlantic menhaden. (Unpublished manuscript.) NMFS Center for Estuarine and Menhaden Research, Beaufort, NC 28516.

Larval menhaden were most abundant in March, prejuveniles in late March and April, and juveniles by the beginning of May (Wilkens and Lewis, 1971). Large catches of larval and prejuvenile menhaden within the freshwater-low salinity zone (Table 2) suggest that favorable conditions for growth are present.

Condition factors (W/L^b, where W = weight in mg, L = length in mm, and b = value for the slope of weight on length for each growth stanza) of larvae and prejuveniles increased with time as the result of growth and development. The apparent lack of growth of larvae and prejuveniles in the low salinity-freshwater zone during April is probably due to large numbers entering this zone, putting on fast growth, moving out of the zone, and being replaced by new groups (Tables 2 and 3). Juveniles, which have the same body form as adults and which are scattered in schools throughout the estuary, showed no change in condition factor with time or salinity.

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TABLE 2.—The distribution and mean total length (mm) of menhaden by date collected, kilometers upstream from Bogue Inlet, and salinity (‰) in the White Oak River estuary, March-August 1969.

	Date 1969										
	Mar. 17	Mar. 27	Apr. 1	Apr. 9	Apr. 16	May 1	May 14	May 27	June 26	July 16	Aug. 27
16 kilometers:											
Salinity	—	0	1.5	4.1	8.0	5.2	13.7	15.4	1.8	10.2	15.1
Abundance index[1]	--	4.3	298.4	48.8	111.0	279.1	0.1	5.2	4.2	4.6	0.3
Mean total length	--	28.5	28.9	30.0	29.2	32.1	--	42.4	53.4	58.8	--
18 kilometers:											
Salinity	1.5	0	0.2	0.1	3.8	1.8	7.4	11.7	0.2	3.0	8.9
Abundance index	9.6	0.4	1,053.4	497.7	526.5	155.2	0.4	1.1	16.3	6.6	0
Mean total length	29.9	--	28.5	27.5	30.8	30.5	--	--	43.5	51.0	--
21 kilometers:											
Salinity	0.2	0	0	0	1.2	--	4.2	--	--	--	--
Abundance index	48.7	0	54.2	65.3	0	--	0.5	--	--	--	--
Mean total length	30.8	0	28.3	27.2	--	--	--	--	--	--	--
24 kilometers:											
Salinity	0	0	0	0	0	0	1.5	4.4	0	0	0.5
Abundance index	13.3	1.8	6.0	1.5	1,533.3	392.6	0.7	13.9	0.4	1.4	1.0
Mean total length	30.1	29.6	29.2	26.6	28.5	29.4	--	42.6	--	--	--
28 kilometers:											
Salinity	0	0	0	0	0	0	0	0.6	0	0	0
Abundance index	0	0.5	1.4	0.2	0.6	0	0.1	12.1	0.3	0.2	0
Mean total length	--	--	29.5	--	--	--	--	41.8	--	--	--
31 kilometers:											
Salinity	0	--	0	0	0	0	0	0	0	--	--
Abundance index	0	--	0.3	10.3	0	0	0	1.0	0	--	--
Mean total length	--	--	--	29.1	--	--	--	--	--	--	--

[1] Abundance index is the number of young menhaden for 100^3 of water.

TABLE 3.— Mean condition factors of young Atlantic menhaden collected in the White Oak River estuary, N.C., in 1969.

	Date	Salinity (‰)							
		0	0.1-0.9	1.0-1.9	2.0-2.9	3.0-3.9	4.0-4.9	5.0-5.9	>6.0
	1969								
Larvae	Mar. 17	0.292	0.303	0.253	--	--	--	--	--
	Mar. 27	0.293	--	--	--	--	--	--	--
		0.302	--	--	--	--	--	--	--
	Apr. 1	0.291	0.309	0.331	--	--	--	--	--
		0.332	--	--	--	--	--	--	--
		0.310	--	--	--	--	--	--	--
	Apr. 9	0.331	0.326	--	--	--	0.326	--	--
		0.317	--	--	--	--	--	--	--
		0.355	--	--	--	--	--	--	--
	Apr. 16	0.321	--	--	--	0.357	--	--	0.444
	May 1	0.358	--	--	--	--	--	--	--
Prejuveniles	Mar. 17	0.299	0.305	0.314	--	--	--	--	--
	Mar. 27	0.394	--	--	--	--	--	--	--
		0.376	--	--	--	--	--	--	--
	Apr. 1	0.342	0.387	0.390	--	--	--	--	--
		0.364	--	--	--	--	--	--	--
		0.381	--	--	--	--	--	--	--
	Apr. 9	0.396	0.435	--	--	--	0.420	--	--
	Apr. 16	0.402	--	--	--	0.476	--	--	0.516
	May 1	0.497	--	0.599	--	--	--	0.547	--
	May 27	--	0.555	--	--	--	--	--	0.498
Juveniles	May 27	--	0.551	--	--	--	0.517	--	0.507
	June 26	--	0.526	0.540	--	--	--	--	--
	July 16[1]	--	--	--	--	0.542	--	--	0.535

[1] Sample sizes after July 16 were too small to show trends.

GROWTH OF PREMIGRATORY CHINOOK SALMON IN SEAWATER

BERNARD M. KEPSHIRE, JR., AND WILLIAM J. MCNEIL[1]

ABSTRACT

A potential demand exists in sea farming for premigratory juvenile Pacific salmon that have been acclimated to seawater. This paper reports experiments on growth of premigratory chinook salmon (*Oncorhynchus tshawytscha*) acclimated to water of 33‰ salinity and lower and describes a simple mathematical model to evaluate rate of growth. Although chinook salmon raised in these experiments experienced low mortality in water of high salinity, their growth slowed. Reasons for slow growth at high salinity are discussed.

Pacific salmon reproduce in fresh water, but only two species—pink (*Onchorhynchus gorbuscha*) and chum (*O. keta*) salmon—survive direct transfer as fry from fresh water to full-strength seawater (Weisbart, 1968). The ocean serves as the early nursery ground for these two species. The other species—including sockeye (*O. nerka*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon—require freshwater nursery areas.

Juvenile salmon undergo a period of adjustment when they first enter the sea in order to regulate water and salts in body fluids and tissues. This adjustive phase for chum salmon fry lasts about 30 hr and is characterized by an immediate depression of activity, increased concentration of salts in body fluids, and dehydration of body tissues (Houston, 1959). A slightly longer adjustive phase of 36 to 40 hr has been reported for yearling coho salmon (Conte et al., 1966; Miles and Smith, 1968).

Early exposure to water of low salinity can "trigger" the physiological adaptation to seawater of salmon species which typically remain in fresh water for several months as juveniles. Acclimation of premigratory young chinook salmon to water of 30‰ salinity by exposing them to gradual increments in salinity has been described by Wagner et al. (1969). Black (1951), Coche (1967), and Otto (1971) found also that coho salmon fry were better able to tolerate water of high salinity after having first been exposed to water of low salinity.

Other evidence suggests that the growth of juvenile coho and chinook salmon is influenced by salinity. Coho salmon fry were observed by Canagaratnam (1959) to grow faster in water of 12 to 18‰ than in fresh water. Otto (1971) reported faster growth of juvenile coho salmon at 5 and 10‰ salinity than at higher salinities or in fresh water. Bullivant (1961) found no significant difference in growth of juvenile chinook salmon in water of 0 and 18‰ salinity. However, Bullivant's fish grew more slowly at 35‰ salinity than at the two lower salinities.

This paper reports comparisons of the growth of juvenile chinook salmon raised in water ranging in salinity from 0 to 33‰. The experiments were conducted at the Oregon State University Port Orford Marine Research Laboratory, Curry County, Oreg.

GENERAL PROCEDURES

Two groups of chinook salmon used in these experiments were obtained as eyed eggs from the Fish Commission of Oregon, Elk River Hatchery, in winter 1969. Group I fish were divided into five subgroups of 200 each on February 24 (47 days after hatching). Group II fish were divided into six subgroups of 300 each on March 5 (18 days after hatching). Individual subgroups were introduced to water of

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increasing salinity according to the schedules outlined in Tables 1 and 2.

Both groups of fish received the Oregon Moist Pellet diet. The young salmon were fed five times daily beginning 30 days after hatching. After the fish had attained an average weight of 1 g, the frequency of feeding was reduced to three times daily. They were provided more food than they would consume at each feeding.

Fish were raised in 100-gal plywood tanks which were lined with fiber glass. Water was introduced to each tank at the rate of one-half gallon per min. Incoming fresh and salt water were premixed in head tanks to obtain desired salinities. Salinities were calculated from the proportions of premixed seawater and fresh water, and density of water in fish tanks was measured periodically with hydrometers to insure that salinities remained at their calculated levels.

The first experiment (Group I fish) began on January 8 with newly hatched alevins. Group I fish first received food on February 7, and selected subgroups were exposed to water of 9 or 17‰ salinity beginning on February 24. The five subgroups were first weighed on February 27. The experiment ended on May 7.

The second experiment (Group II fish) began on February 16 with newly hatched alevins. All six subgroups of fish were first exposed to water of 5 or 9‰ salinity on March 6 while still in the alevin stage, and they remained at these salinities for 18 days. The fish were first fed on March 18 and first weighed on April 7. The experiment ended on May 6.

Mortality of the 11 subgroups of fish during the test periods ranged from 0 to 6% of the original number of fish placed in the tanks. Even the maximum mortality (6%) was considered to have no appreciable effect on the comparisons of growth.

The average wet weight of fish in each subgroup was determined at 14-day intervals from random samples of 30 fish. Excess water was blotted from anesthetized fish before weighing. Fish were weighed separately in a flask containing a known weight of water and were returned to their respective tanks after each weighing.

TABLE 1.—Exposure of Group I chinook salmon to water of increasing salinity. Date of hatch—January 7, 1969.

Subgroup	Age (days after hatching) at which fish were placed in water[1] of given salinity		
	47	66	80
	‰	‰	‰
Ia	0	0	0
Ib	9	17	17
Ic	17	17	33
Id	17	24	33
Ie	9	24	33

[1] Temperature of incoming water averaged 10.7° C for fresh water and 10.8° C for seawater.

TABLE 2.—Exposure of Group II chinook salmon to water of increasing salinity. Date of hatch—February 15, 1969.

Subgroup	Age (days after hatching) at which fish were placed in water[1] of given salinity			
	18	36	54	66
	‰	‰	‰	‰
IIa	5	18	18	18
IIb	9	18	18	18
IIc	5	18	25	33
IId	5	18	25	33
IIe	9	18	25	33
IIf	9	18	25	33

[1] Temperature of incoming water averaged 11.9° C for fresh water and 12.0° C for seawater.

OBSERVATIONS ON GROWTH

Growth rate was calculated for each subgroup from the periodic measurements of wet weight. Growth was assumed to be exponential over each period considered, and a value for the daily increment in body weight, which can be expressed as a percent of body weight per day, was obtained from the expression

$$\frac{W_t}{W_0} = (1 + h)^t \qquad (1)$$

where W_t = weight at the end of the period,
W_0 = weight at the beginning of the period,
h = the compounded daily increment of body weight, and
t = days.

It is convenient to solve equation (1) for $(1 + h)$ by converting the terms to common logarithms and taking the antilog, i.e.

$$\log (1 + h) = \frac{\log W_t - \log W_0}{t} . \qquad (2)$$

To clarify the concept of daily increment of body weight, fish that can maintain an increase in body weight of 2.0 and 3.0% per day, for example, will double their weight in approximately 35 and 23 days, respectively.

Fish held in water of 0, 17, and 18‰ salinity grew at a faster rate and were heavier at the end of the experiments than fish of the same age transferred to water of 24, 25, and 33‰ salinity. The observed mean weight of fish in individual subgroups is plotted against age of fish in Figure 1.

Equation (2) can be rewritten in linear form to calculate statistics which are useful for making comparisons of rate of growth among test groups of fish. The linear model is:

$$(\log W_t - \log W_0) = \log (1 + h) \cdot t \quad (3)$$

Slope of the regression line is given as log $(1 + h)$. This model requires the regression line to pass through the origin since $(\log W_t - \log W_0) = 0$ at $t = 0$.

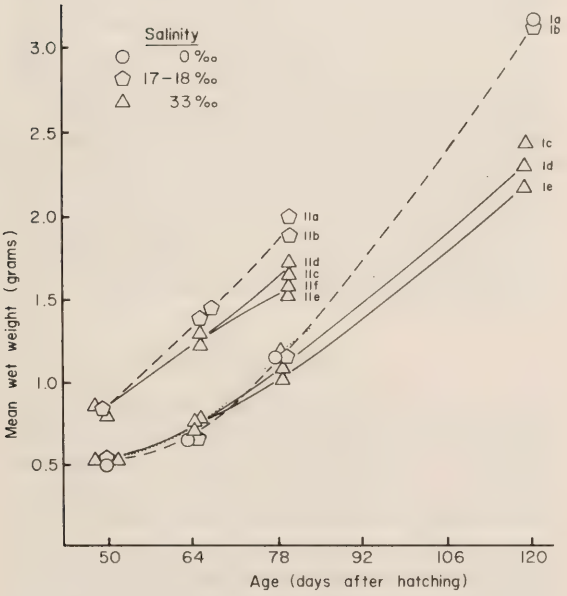

FIGURE 1.—Growth in weight of experimental subgroups of juvenile chinook salmon.

Group I fish were weighed on six occasions over a period of 70 days. We have estimated values of log $(1 + h)$ and h for each of the five subgroups of Group I by calculating the five regressions of $(\log W_t - \log W_0)$ on t. Because the weight of Group II fish was measured on only three occasions, we have not applied a similar analysis to the second experiment.

Application of regression methods to observations on Group I fish indicates that fish in fresh water and water of 17‰ salinity (Subgroups Ia and Ib) grew at a significantly faster rate than fish exposed to water of 33‰ salinity (subgroups Ic, Id, and Ie). Equations for the five subgroups are given in Table 3 along with the 95% confidence interval estimates of log $(1 + h)$ and the approximate confidence interval estimates of h. Figure 2 shows growth curves for the fastest (Subgroup Ia) and slowest (Subgroup Ie) growing fish. The periodic measurements of weight are plotted in Figure 2 to show their correspondence with the growth curves calculated by use of equation (1).

DISCUSSION

Chinook salmon used in these experiments were exposed to salt water much earlier in life than they normally would experience in nature. Group I fish were acclimated to high salinity (24‰) 66 days after hatching and 36 days after commencement of feeding. Group II fish were acclimated to high salinity (25‰) 54 days after hatching and 24 days after commencement of feeding. There were only 66 deaths (3.7%) among the 1,800 fish which had been exposed to salinities of 24, 25, and 33‰ for periods of 25 and 54 days.

The average rate of growth in water of high salinity (24‰ and above) varied between 2.1 and 2.3% increment in body weight per day. These fish doubled their weight in 30 to 33 days. The average rate of growth in water of low salinity (17‰ and 0‰) was 2.6 and 2.7% per day. These fish doubled their weight in 26 to 27 days.

Although these experiments demonstrate that juvenile chinook salmon can be acclimated to full-strength seawater in an early age, it is apparent that water of high salinity causes a reduced rate

TABLE 3.—Regression of (log W_t − log W_0) on time for Group I fish. The approximate 95% confidence interval estimates of h are taken from the confidence limits of log $(1 + h)$.

Sub-group	Regression equation	95% confidence limits of log $(1 + h)$	Approximate 95% confidence limits of h
Ia	(log W_t − log W_0) = 0.01168t	0.01168 ± 0.00099	2.7 ± 0.2%/day
Ib	(log W_t − log W_0) = 0.01118t	0.01118 ± 0.00084	2.6 ± 0.2%/day
Ic	(log W_t − log W_0) = 0.01006t	0.01006 ± 0.00087	2.3 ± 0.2%/day
Id	(log W_t − log W_0) = 0.00945t	0.00945 ± 0.00077	2.2 ± 0.2%/day
Ie	(log W_t − log W_0) = 0.00880t	0.00880 ± 0.00042	2.1 ± 0.1%/day

of growth. Reduced growth may come about in part because the young salmon expend more energy to maintain an osmotic homeostasis in water of high salinity than in water of low salinity.

Chinook salmon blood is isotonic with water of salinity between 10 and 13‰ (Coche, 1967). Houston (1959) thought that the increased energy demands for osmoregulation combined with possible inhibition of electrolyte-sensitive components of the neuromuscular system might contribute to reduced growth of young salmon in water of high salinity. There is the further possibility that endocrine systems which are associated with osmoregulation and growth in water of high salinity are not fully functional in premigratory juvenile salmon (Saunders and Henderson, 1970).

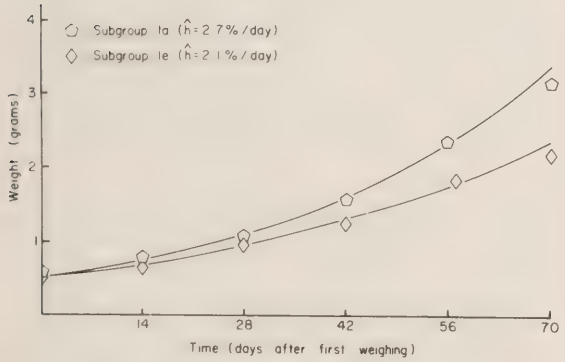

FIGURE 2.—Calculated growth curves for chinook salmon from subgroups Ia and Ie as calculated from equation (1). The observed growth is plotted to illustrate correspondence with calculated curves. "h" is the compounded daily increment of body weight.

The acclimation of premigratory chinook, coho, and sockeye salmon to seawater may find future applications in aquaculture. Possibilities include the early release of young salmon from hatcheries into open ocean pastures to reduce costs of feeding and handling and to increase hatchery production. Other possibilities are to pen young salmon in saltwater bays or estuaries (Garrison, 1965; Mahnken et al., 1970) or to place them in raceways receiving waste salt water from coastal thermal-electric stations (McNeil, 1970).

Large-scale aquaculture systems, similar to one under development in the Canadian Maritime Provinces (Gunstrom, 1970), would most likely benefit from early acclimation of juvenile salmon to seawater. The release of premigratory juvenile chinook salmon acclimated to seawater should also be tested at hatcheries equipped with seawater pumping systems. The effects of early acclimation on ocean survival is unknown, but the greater availability of food and space in the ocean than in freshwater conceivably would provide potential advantages to juvenile salmon which had been acclimated to seawater.

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EFFECT OF ENCROACHMENT OF WANAPUM DAM RESERVOIR ON FISH PASSAGE OVER ROCK ISLAND DAM, COLUMBIA RIVER

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ABSTRACT

The filling of Wanapum Reservoir in 1964 flooded the lower sections of the three fish ladders at Rock Island Dam, 61 km upstream from Wanapum Dam on the Columbia River. To maintain fish passage under the new hydraulic conditions, the lower portions of the center and left-bank fish ladders of Rock Island Dam were rebuilt and a new sequence of spill patterns inaugurated. The effectiveness of these modifications was evaluated by comparing results from a series of tagging experiments conducted in 1964-65 on spring chinook salmon (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*) with the results of similar experiments in 1954-55 before Wanapum Dam was built. These comparisons indicated fish passage over Rock Island Dam had improved substantially between 1954-55 and 1964-65; tagged fish traveled over the dam in a shorter time, and higher percentages of the tagged groups were sighted passing over the dam under postencroachment conditions.

Successful reproduction of Pacific salmon (*Oncorhynchus* spp.) and steelhead trout (*Salmo gairdneri*) requires that sufficient numbers of adults in suitable physical condition reach the spawning grounds. Serious consequences can result from delays en route. Thompson (1945), for example, showed that very few of the sockeye salmon (*O. nerka*) that were delayed more than 12 days by the Hell's Gate rock slide (Fraser River, British Columbia) reached their spawning grounds. Thompson also suggested that shorter delays reduced the reproductive capability of the survivors. Similarly, man-made facilities such as hydroelectric dams, even though equipped with fish-passage facilities, can act as barriers and thus delay or otherwise interfere with the migratory behavior of salmonids on their way to the spawning grounds.

One of the primary goals of the agencies responsible for conserving the fish resources of the Columbia River is to seek ways of minimizing the effects of dams on the migration and spawning success of the river's populations of salmonids. Although a variety of solutions to the problem of dams impeding the passage of migrating spawners have been proposed and a number of these have been tried in the field, the pool type of ladder has proven to be the only practical means of passing large numbers of adult salmonids over the dams on the Columbia River. Many research studies aimed at improving fish passage have been conducted over the past several decades. One result of this research has been the introduction of a number of improvements in design and operation of the pool-and-weir ladder. In some cases fish passage over ladders can be substantially improved by modification of spill patterns (Leman and Paulik, 1966).

The present study was designed to evaluate the effectiveness of modifications in the fish ladders at Rock Island Dam and changes in the spill pattern which were made after the lower portions of the ladders were flooded by the reservoir of Wanapum Dam. This type of problem is apt to become more common as all existing sites for hydroelectric dams are utilized and the reservoir of one dam begins to encroach on the tailrace of the dam immediately above.

Rock Island Dam, completed in 1934, was the first dam built on the Columbia River. It is in central Washington and about 725 km above the river's mouth (Figure 1). Originally, the dam

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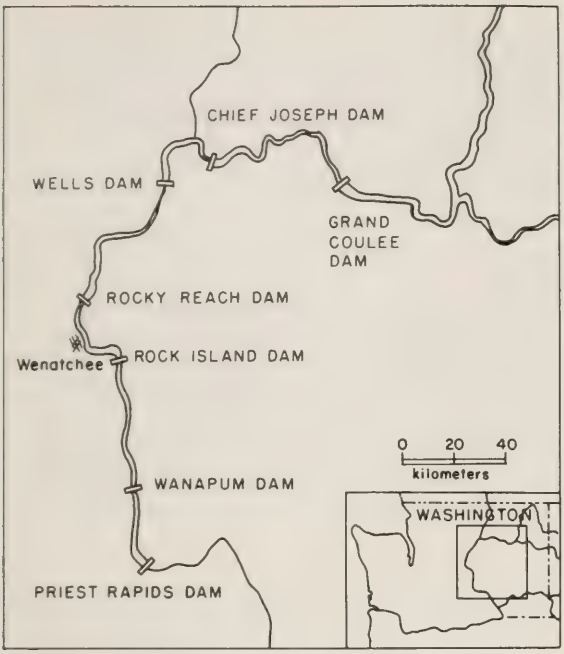

FIGURE 1.—The Columbia River and locations important to the present study.

was provided with two pool- and weir-type fish ladders, one adjacent to each bank. A third was added near the middle of the dam in 1936.

Rock Island Dam was modified during 1951-53. Six new generating units were added to the powerhouse (on the left side of the dam looking downstream), the reservoir was raised about 3.7 m, and regulating lift gates were installed in spillway bays 16-37 on the right side of the dam (Figure 2). Turbine discharge was increased from about 793 to 2,265 m^3 per sec, the fish ladders were altered to enable them to function at the new reservoir level, and the attraction flow at the entrance to the left ladder was increased to counteract the increased discharge from the turbines. Although the fishery agencies requested changes at the lower end of the right ladder to provide better entrance conditions and additional attraction flow, no immediate action was taken to implement these requests.

The Federal Power Commission, in granting permission for the modification of the dam, reserved the right to require alteration of the lower end of the right-bank ladder if substantial evidence were presented to show that alteration was necessary to protect runs of anadromous fish. Any such alteration was to begin before December 1, 1960.

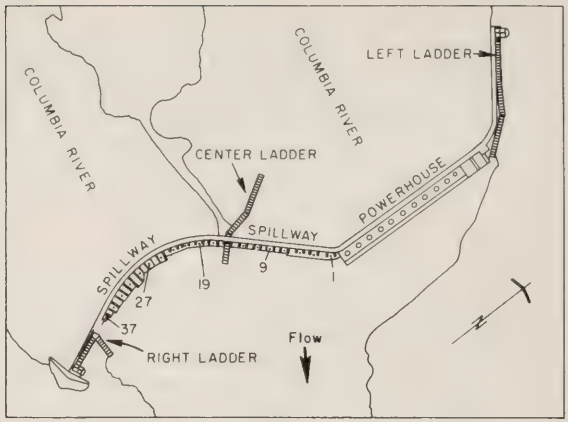

FIGURE 2.—Rock Island Dam showing locations of the fish ladders, powerhouse, and spillway bays.

To determine whether the dam caused loss or delay to the runs and whether loss or delay was associated with the right-bank fishway, tagging studies were conducted in 1954-56. French and Wahle (1966) summarized the results as follows:

> Point estimates of sockeye salmon losses ranged from 0 to 42 percent. Tagging results (one season only) on spring chinook salmon indicated a loss of fish released below the right bank ladder, but no loss when total tag returns from below and above dam releases were compared; data failed to show the dam caused losses of summer chinook. Tagged salmon released below the dam were delayed 2 to 4 days. Altering the right bank fishway may cause more fish to use it, but there is no clear evidence that such alteration will reduce overall loss or delay.[3]

Although the evidence did not indicate that a major overhaul of the right-bank ladder was justified, one relatively minor change was made. In 1956, a concrete wall was built at the entrance to the ladder. This wall replaced a cyclone fence

[3] Seasonal races of chinook salmon (*O. tshawytcha*) in the Columbia River system are classified as spring, summer, or fall chinook depending on the time of year that the adults enter the river to spawn.

which, at high tailwater elevations, appeared to impede the entry of fish into the ladder. The wall also eliminated the surging action across the ladder that occurred under certain combinations of spill pattern and tailwater elevation.

Even after these changes, fishery biologists continued to voice concern over the effectiveness of the right-bank ladder. Some held that hydraulic conditions at the entrance to the right-bank ladder impeded fish passage over the ladder. In 1958, in response to the continuing concern about the fish-passage conditions at Rock Island Dam, the owners of the dam—Puget Sound Power and Light Co. and Public Utility District No. 1 of Chelan County—financed a study to determine if fish passage could be improved by manipulating the spill pattern.

The study showed that fish could be guided to either the right or center ladders by spilling adjacent to the respective ladder. The experiment also indicated, but not conclusively, that when low tailwater elevations prevailed, spilling from gates 35, 36, and 37 (immediately adjacent to the right-bank ladder) confused the fish and interfered with their entry into the ladder (Leman and Paulik, 1966).

The construction in 1960-64 of Wanapum Dam, 61 km downstream, brought about a further change in fish-passage conditions at Rock Island Dam. The lower portions of the fish ladders at Rock Island Dam were flooded by Wanapum Reservoir. This condition, in the judgment of the Federal Power Commission, required certain modifications of the left and center fish ladders. The modifications were completed by 1963—1 year before Wanapum Reservoir was filled. The Commission also directed the owners of Rock Island Dam and of Wanapum Dam (Public Utility District of Grant County) to develop, in cooperation with representatives of the U.S. Department of the Interior and the Washington State Departments of Fisheries and Game, a program for the study and evaluation of the further effects of encroachment by Wanapum Reservoir on fish passage at Rock Island Dam.

It is important to note that the question at hand was the effect of the encroachment of Wanapum Reservoir on fish passage at Rock Island Dam and not the effects of Wanapum Dam on fish passage in the broader sense, i.e., passage over Wanapum Dam itself and passage through the newly formed forebay.

Representatives of the participating agencies formed the "Rock Island Study Group" and engaged the junior author as a consultant to serve as chairman of the group. A major segment of the research program, initiated and supervised by the study group, consisted of a series of tagging experiments conducted under postencroachment conditions. These experiments were so designed that the results would be comparable to results available from preencroachment tagging in 1954-55 (French and Wahle, 1966).[4] The field work was conducted by experienced personnel of the National Marine Fisheries Service (formerly the Bureau of Commercial Fisheries) under the supervision of the senior author.

In this paper we describe tagging experiments at Rock Island Dam in 1964-65 and compare the results to those obtained in the earlier (1954-55) study. The primary purpose is to estimate the differences between the times required for sockeye and spring chinook salmon (*O. tshawytscha*) to move from tagging sites below Rock Island Dam to the counting stations in the three (left, center, and right) fish ladders before encroachment and after encroachment.

EXPERIMENT RATIONALE

The basic experimental measures obtained from this type of tagging are (1) elapsed time from the release of tagged fish below Rock Island Dam to the sighting of tagged fish as they passed through a counting station near the top exit of the fish ladders and (2) the percentage of each release group passing over the dam. The elapsed times include (a) the time, if any, required for tagged fish to recover from possible effects of tagging, (b) the time required to locate and enter the fish ladders, and (c) the time required to ascend the ladders. A statistical analysis of the preencroachment tagging was employed to determine adequate sample sizes and release

[4] French and Wahle also tagged in 1956, but because the tagged fish were released in a different manner and at different locations than in any other year, the 1956 experiments were excluded from our comparisons.

frequencies needed in postencroachment tagging to be 95% certain of detecting a change of one-half day and 99% certain of detecting a change of a full day in elapsed times, if such changes occurred between 1954-55 and 1964-65. If we assume that the basic condition of the tagged fish and the time required for tagged fish to recover from possible effects of tagging did not differ significantly between the 1954-55 and 1964-65 experiments, it follows that changes in elapsed times could be attributed to the ability of tagged fish to find and ascend the fishways. The efficiency of the fish-passage system at Rock Island Dam could thus be compared under pre- and postencroachment conditions. Although travel times were expected to be the most sensitive measure of encroachment effects, it is obvious that any significant drop in the percentage of tagged fish passing over the dam would indicate severe stress under postencroachment conditions.

It might seem unrealistic at first to assume that tagged fish recovered from the possible effects of tagging equally well in the pre- and postencroachment phases of the study. One might expect, for example, that tagged fish were released into faster moving water in 1954-55 and into slower moving water in 1964-65 and that, accordingly, the tagged fish required longer to recover from the effects of tagging in the earlier phase of the study than in the latter. If this were true, we might have ended up measuring differences in recovery time of tagged fish rather than differences in the efficiency of the Rock Island Dam fish ladders.

Although water velocities were not measured at the release sites, velocities measured in a model of Rock Island Dam (Ward, 1965)[5] were not uniformly different under postencroachment conditions than under preencroachment conditions. In fact, velocities at the measuring point nearest the right-bank release site on the simulated model were generally higher after encroachment than before. On the other hand, at the station closest to the left-bank release site, velocities were higher at lower river flows and about the same at higher flows after encroachment.

Observations made during the 1964-65 experiments revealed that large numbers of tagged fish tended to remain close to shore in protective eddies. According to French, tagged fish behaved similarly during the 1954-55 experiments.[6] These observations tend to support the assumption that tagged fish recovered from tagging equally well in 1954-55 and 1964-65.

The flooding of the lower portions of the fish ladders at Rock Island Dam by Wanapum Reservoir was not the only factor affecting fish passage that changed between 1954-55 and 1964-65. Riprap was added to the left bank of the river below the dam, and the left and center fish ladders were modified extensively. Figures 3 and 4 show Rock Island Dam before and after Wanapum Reservoir had been filled. New spill patterns designed to enhance fish passage were in effect throughout most of the 1964 and all of the 1965 tagging. The basic pattern was developed from findings of the 1958 study (Leman and Paulik, 1966) and modified slightly after experiments with the model of Rock Island Dam (Ward, 1965, see footnote 5).

METHODS AND MATERIALS

The basic experimental procedure was as follows: salmon were trapped as they passed over the left ladder, transported to the release sites approximately 300 m below Rock Island Dam on either side of the river, then tagged and released. Fish counters at the dam recorded the tags as the tagged fish passed the counting boards after reascending the ladders.

TAGGING

Two different traps were used to capture the salmon. Sockeye were captured as they entered a trap placed at the upstream edge of the counting board in the left-bank fish ladder. Chinook salmon, which would not enter this trap, had to

[5] Ward, David A. 1965. Hydraulic model studies of the Rock Island fish attraction facilities. Wash. State Univ., Pullman, Div. Ind. Res., Inst. Technol., Res. Rep. 65/9-43. Vol. I—20 p., 29 fig., Append. I-II; Vol. II—23 fig. (Processed.)

[6] Personal communication, Robert R. French, Fishery Biologist, Natl. Mar. Fish. Serv., Northwest Fish. Cent., Seattle, Wash.

FIGURE 3.—Rock Island Dam before Wanapum Dam had been built.

FIGURE 4.—Rock Island Dam after Wanapum Dam had been built. Note how the rocks and the lower portion of the right-bank fish ladder, visible below the dam in Figure 3, have been inundated in Figure 4.

be taken in a larger floating trap positioned at the upstream end of the ladder.

A conventional 1,000-gal (3.79-m^3) tank truck transported sockeye salmon in 1964 and 1965 and chinook salmon in 1965 but was not available for the 1964 chinook salmon experiments. Instead, we used 1.2 m by 1.2 m by 1.1 m plywood boxes, equipped with aeration systems and mounted on ¾-ton (680-kg) trucks. These units were suitable for transporting fish to the adjacent left-bank release site but inadequate for moving more than seven or eight fish per unit to the opposite bank via Wenatchee, Wash.,—a 48-km trip that took about ½ hr. Because of this limitation, only one-half as many chinook salmon were released on the right bank as on the left bank in 1964.

Each batch of fish liberated was distinctively marked. Several types and colors of tags were used. Petersen plastic disks were used either alone or in combination with plastic bars and vinyl streamers. Nickel pins, inserted through the body just below the dorsal fin, provided the attachment. Tags were applied in pairs, so that the same color and type of tag showed on both sides of the fish. Tagging time seldom exceeded 30 sec per fish.

ARTIFICIAL MANIPULATION OF SPILL PATTERN, AUGUST 3-5, 1964

The spill pattern throughout most of the 1964 and 1965 tagging was developed from results of experiments at Rock Island Dam in 1958 (Leman and Paulik, 1966) with subsequent refinements from a model study in 1964 and 1965 (Ward, 1965, see footnote 5). On August 3-5, 1964, however, gates 16 to 18 (adjacent to the center ladder) were closed and gates 34, 36, and 37 (adjacent to the right-bank ladder) were opened. This departure from the recommended spill pattern was undertaken to measure its effect on the passage of tagged fish over the dam.

TAG OBSERVATION AND DATA RECORDING

Four steps were taken to insure the accuracy of the tag observations: First, hydroscopes (floating "windows") were installed over the counting boards on the right- and left-bank ladders to suppress glare and surface disturbance. Second, all fish counters were tested for color blindness. Third, samples of tags were mounted on the tally boards to facilitate instant recognition and recording of the tags. Fourth, fish counters were systematically rotated between ladders to distribute any bias by the counters between the ladders.

The gates in the fish ladders were open and the passing fish were counted 16 hr a day—5:00 AM to 9:00 PM—during these experiments. The half-day units used to measure travel times were adapted to the counting schedule. Fish observed during the same 8-hr period in which they were released were assigned a travel time of one-quarter day or 0.5 half-day. Fish released just before noon (as most were) were given a travel time of 0.5 half-day, if observed the same day, or a time of 1.0 half-day if observed the next morning. Tag observations were grouped by tag combination, ladder, and travel time in half days. Data were punched on IBM cards—one card containing the release and recovery data for each fish. The numbers of tagged salmon released below Rock Island Dam and later observed passing the dam in 1954, 1955, 1964, and 1965 are summarized in Table 1.

TABLE 1.—Numbers of salmon that were tagged and released below Rock Island Dam in 1954, 1955, 1964, and 1965, and the numbers and percentages of tagged fish that were later observed passing over the dam's fish ladders.[1]

Species of salmon	Year	Fish tagged and released below dam	Tagged fish observed passing dam	
		no.	*no.*	*%*
Spring chinook	1954	155	60	38.7
	1955	157	94	59.9
	1964	103	93	90.3
	1965	311	285	91.6
Sockeye	1954	1,485	1,176	79.2
	1955	1,176	793	67.4
	1964	951	895	94.1
	1965	679	623	91.8

[1] The numbers of spring chinook salmon released in 1954 and 1955 differ from those reported by French and Wahle (1966). They used the July 13 date suggested by Fish and Hanavan (1948) as the termination of the spring run and the beginning of the summer run. We used the scale method described by Koo and Isarankura (1967) to determine that the dates of least overlap between the two races were July 30, 1954, and July 8, 1955. We believe that our separations, based on the more recent study, are the more accurate.

TAG OBSERVATIONS AT ROCK ISLAND DAM, 1964 AND 1965

The 1964 and 1965 data are treated by species—spring chinook salmon first, followed by sockeye salmon. In a later section these data will be compared to the 1954 and 1955 results to determine the effects of encroachment of Wanapum Reservoir on fish passage at Rock Island Dam.

SPRING CHINOOK SALMON

The tag release and tag observation data for 1964 and 1965 are presented in Table 2. Included are the date and location of release, the number of fish tagged, the release area, and the number and mean travel time of tagged fish subsequently observed passing Rock Island Dam. Logarithmically transformed data are used throughout this paper for analysis of travel time; means are geometric means.

Three times as many chinook (311) were tagged in 1965 as in 1964 (103). The small number released and the short duration of the tagging period in 1964 (May 19-27) can be attributed to difficulties in completing the access roads, difficulties with the trapping and transportation systems, and a shortage of fish in the left-bank ladder—the ladder where the trap was located. Tagging was from May 16 to June 9, 1965. The 1965 data are grouped, somewhat arbitrarily, into five time periods.

Percentage Observed

The overall percentages of tagged chinook salmon subsequently observed passing over Rock Island Dam were 90.3 in 1964 and 91.6 in 1965. Variability among the release groups was high, ranging from 67 to 129% in 1964 and 60 to 115% in 1965. It is noteworthy that the number observed exceeded the number released for 6 of the 24 releases over the two tagging seasons.

TABLE 2.—Numbers of chinook salmon that were tagged, released below Rock Island Dam and the numbers and mean travel times of tagged fish that were later observed passing over the dam's fish ladders, 1964 and 1965.

			Number of fish tagged and released below dam		Number and mean travel time in half-days of tagged fish observed passing dam							
					Left ladder		Center ladder		Right ladder		Total[1]	
Year	Period	Date	Left bank	Right bank	No.	Travel time	No.	Travel time	No.	Travel time	No.	Travel time
1964		May 19	17	--	10	14.8	5	16.8	7	8.5	22	12.8
		May 19	--	15	6	6.0	6	8.7	1	4.0	13	6.9
		May 20	13	--	7	13.2	6	13.4	2	14.8	15	13.5
		May 20	--	17	6	18.1	3	5.3	4	6.6	13	10.0
		May 21	27	--	9	10.5	7	4.2	4	8.1	20	7.2
		May 21	--	5	1	7.0	3	12.6	0	--	4	10.9
		May 27	9	--	4	9.9	0	--	2	8.7	6	9.5
1965		May 16	5	--	1	2.5	3	3.4	1	2.5	5	3.0
	I	May 18	5	--	2	11.5	2	4.0	1	2.0	5	5.3
		May 21	--	19	12	6.8	4	2.7	3	4.0	19	5.1
		May 22	41	--	33	5.4	9	15.8	5	5.7	47	6.6
		May 23	--	11	8	7.0	3	5.2	0	--	11	6.4
		May 24	9	--	4	4.7	0	--	2	2.5	6	3.8
	II	May 24	--	25	17	7.7	6	4.7	3	2.5	26	6.0
		May 25	8	--	5	3.1	2	22.5	2	12.5	9	6.6
		May 26	15	--	8	4.8	0	--	1	0.5	9	3.7
	III	May 27	--	30	23	8.2	4	5.9	5	3.9	32	7.0
		May 28	28	--	16	9.1	4	15.5	5	3.7	25	8.3
	IV	May 31	21	--	10	6.7	2	5.2	2	6.5	14	6.5
		June 1	--	27	14	6.4	4	4.1	4	2.4	22	4.9
	V	June 4	10	--	5	2.7	3	8.0	0	--	8	4.1
		June 4	--	22	11	6.9	2	6.6	5	2.3	18	5.0
	VI	June 8	--	22	12	3.9	3	5.1	5	3.2	20	3.9
		June 9	13	--	8	6.5	1	20.5	0	--	9	7.3

[1] The total number observed may exceed the number tagged. See text (p. 132) for explanation.

Possible explanations include the misidentification of tags by the counters and multiple observations of the same tagged fish that passed over the dam, fell back, and survived to pass over the dam again. The "falling back" of salmon over dams is a frequent occurrence on the Columbia River (Johnson, 1965),[7] although recent studies[8] have shown the magnitude of such fallback is not large (usually less than 5%).

The percentages of tagged fish recovered by release location (releases pooled by location within years) were not consistent for the 2 years. In 1964 the percentage of tagged fish released on the left bank and subsequently observed exceeded that of the right bank—95.5 to 81.1. In 1965 the comparable percentages were 88.4 and 94.9, respectively.

Distribution by Ladder

Of the tagged fish sighted in 1964, nearly one-half (46.2%) chose the left ladder; the center and right ladders lured 32.3 and 21.5%, respectively. In 1965, 66.3% chose the left ladder, 18.2% the center ladder, and 15.4% the right ladder. Distribution between ladders was basically the same for each release site within, but not between, years. The percentages observed in the left ladder were 47.6 and 43.3 for the left- and right-bank releases in 1964 but considerably higher (67.2 and 65.5) for fish released from the left and right banks, respectively, in 1965. However, in both years similar percentages of the fish not using the left ladder chose the center ladder (60.0 in 1964 and 54.1 in 1965).

Between-period comparisons are possible for 1965 only when the percentage of tagged fish using the left-bank ladder remained very consistent from period to period, varying only from 61.5 to 69.0.

[7] Johnson, James H. 1965. Fallback of adult chinook salmon at Ice Harbor Dam spillway, May 1964. Final Report to U.S. Army Corps of Engineers for Research Contract No. DA-45-164-CIVENG-63-286. Bur. Commer. Fish., Fish-Passage Research Program, Seattle, Wash., 16 p. (Processed.)

[8] Personal communication with Charles Junge of the Oregon Fish Commission with regard to experiments with tagged chinook salmon at Bonneville Dam during 1970.

Travel Time from Release to Observation in Fish Ladders

Travel times—by date of release, release location, and ladder in which the tagged spring chinook salmon were sighted—are presented in Table 2. Because of the small numbers of fish involved in the 1964 tests, their value is limited. The 1965 experiments provided the most sensitive analysis of the time required for tagged fish to pass over Rock Island Dam under encroachment conditions.

Results of analysis of variance tests of the hypothesis of no difference in mean travel time between fish released on the right and left banks in 1965 are summarized in Table 3. Regardless of how the data were grouped—whether travel times of the right-bank and the left-bank releases were compared period by period, whether adjacent periods were combined, or whether all periods were pooled—no statistically significant differences were found. It is noteworthy, however, that the mean passage time for fish released from the right-bank site was less than for fish released at the left-bank site. Thus, fish released from the right bank were finding and passing over the ladders at least as fast as, if not faster than, those released from the left bank.

TABLE 3.—Analysis of variance tests of the hypothesis that spring chinook salmon, tagged and released on the left bank below Rock Island Dam in 1965, traveled over the Rock Island Dam fish ladders equally as fast as fish released on the right bank below the dam.

Periods	Mean travel time in half-days, all ladders combined		*F*-statistics (1 and 268 df)
	Left-bank releases	Right-bank releases	
I	6.081	5.130	0.32 N.S.[1]
II	4.630	6.159	0.93 N.S.
III	8.249	7.009	0.29 N.S.
IV	6.454	4.940	0.48 N.S.
V	4.054	5.048	0.21 N.S.
VI	7.342	3.855	2.03 N.S.
			F-statistics (1 and 279 df)
I and II	5.609	5.789	0.03 N.S.
III and IV	7.553	6.078	0.84 N.S.
V and VI	5.553	4.380	0.50 N.S.
			F-statistics (1 and 283 df)
I-VI	6.097	5.486	0.63 N.S.

[1] N.S. = Not significant.

TABLE 4.—Analysis of variance tests of the hypothesis that spring chinook salmon, tagged and released below Rock Island Dam in 1965, traveled over the right fish ladder at Rock Island Dam equally as fast as those traveling over the left and center ladders.

Ladders compared	Mean travel time in half days, release areas combined			F-statistics[1] (1 and 268 df)
	Left ladder	Center ladder	Right ladder	
Right vs. left	6.210	--	3.396	10.60**
Right vs. center	--	6.929	3.396	9.86**

[1] ** = Highly significant at the 0.01 level, reject hypothesis of equal travel times, and conclude that travel time was significantly less through the right ladder.

We also analyzed the 1965 data on a ladder by ladder basis. Although the data, even when compared on a period by period basis, are too limited to provide a sensitive comparison of the mean passage times between fish using the different ladders, they did reveal that in every period fish moved over the right ladder faster than over either the center or left ladder. Mean passage times for right ladder versus the left ladder and right ladder versus the center ladder (all periods and both release sites pooled) are compared in Table 4.[9] The data have been adjusted for simultaneous tests according to the method described by Dunn (1961). The differences shown in Table 4 are highly significant. Thus the hypothesis that spring chinook salmon traveled from the tagging sites over the right ladder equally as fast as over the left ladder is strongly rejected as is the same hypothesis for the right versus the center ladder. In both cases the mean passage times are significantly less for fish using the right ladder. This means that ladder choice was the only observed factor clearly affecting passage time. Similar trends were noted in 1964. Mean passage time over the right ladder was less than for either the left or center ladders.

The overall travel time in 1965 (5.8 half-days) was shown by an analysis of variance test to be significantly less than that of 1964 (9.8 half-days). The F-value for this test was 17.72 with 1 and 165 degrees of freedom.

[9] Because the passage of fish over the right-bank fish ladder had been a source of controversy among fishery biologists, we directed special attention to the right-bank ladder in the present study.

SOCKEYE SALMON

Fewer sockeye salmon were tagged in 1965 than in 1964. Analysis of the 1964 data revealed that the precision desired could still be achieved if sample sizes were reduced from 100 to 75 fish per release in each year. The tagging season was divided into five periods. With one exception, each of these periods contained releases from the left and right banks. During period IV in 1965, both releases were from the left bank.

Tagging was from July 15 to August 5 in 1964 and from July 14 to August 4 in 1965. Tag release and tag observation data are presented in Table 5.

Percentage Observed

The percentages of tagged sockeye from individual releases observed passing Rock Island Dam were similar for 1964 and 1965. The percentage ranged from 84.3 to 120.8 in 1964 and from 81.2 to 98.8 in 1965. Overall, 94.1% of the tagged fish were observed in 1964 and 91.8% in 1965. Percentages observed from left-bank releases were not significantly different from those released on the right bank in either year—94.8 (left bank) versus 93.3 (right bank) in 1964 and 91.5 (left bank) versus 92.0 (right bank) in 1965.

Distribution by Ladder

Distribution by ladder was similar in both years. Of the tagged fish sighted, 55.6% used the left ladder in 1964 and 53.1% in 1965. The center ladder took 20.7 and 23.6% and the right ladder 23.7 and 23.3% in the 2 years, respectively. For the left- and right-bank releases, respectively, the percentages using the left ladder were 54.1 and 57.4 in 1964. Comparable percentages were 55.4 and 50.7 in 1965. Fish not choosing the left ladder were fairly evenly distributed between the center and right ladders in both years.

The between-period consistency of the percentage of tagged sockeye salmon using the preferred left ladder was less evident than for chinook salmon. For sockeye salmon, the

TABLE 5.—Numbers of sockeye salmon that were tagged, released below Rock Island Dam and the numbers, and mean travel times of tagged fish that were later observed passing over the dam's fish ladders, 1964 and 1965.

Year	Period	Date	Number of fish tagged and released below dam		Number and mean travel time in half-days of tagged fish observed passing dam							
					Left ladder		Center ladder		Right ladder		Total[1]	
			Left bank	Right bank	No.	Travel time	No.	Travel time	No.	Travel time	No.	Travel time
1964	I	July 15	76	--	21	2.7	16	2.2	40	2.4	77	2.4
		July 16	24	--	16	2.2	9	1.9	7	2.0	29	2.1
		July 17	--	113	48	5.9	29	4.8	29	6.8	106	5.8
	II	July 21	--	70	35	4.9	8	4.9	16	3.0	59	4.3
		July 22	104	--	59	3.4	16	2.8	15	4.1	90	3.4
		July 23	--	89	48	5.7	20	3.3	16	4.8	84	4.8
	III	July 28	92	--	45	1.6	25	1.3	19	3.2	89	1.7
		July 30	--	80	56	5.0	20	3.3	11	5.5	87	4.6
	IV	July 31	85	--	53	2.3	16	3.4	13	3.3	82	2.7
		August 3	70	--	38	4.4	10	2.8	15	5.6	63	4.4
	V	August 4	--	96	53	4.8	13	3.3	16	5.6	82	4.6
		August 5	52	--	26	4.1	6	2.8	15	3.1	47	3.6
1965	I	July 14	71	--	38	3.1	8	3.8	23	2.4	69	2.9
		July 15	--	68	38	4.2	9	2.3	20	3.5	67	3.7
	II	July 19	81	--	51	4.6	7	4.2	22	4.7	80	4.6
		July 20	--	76	43	4.1	6	2.9	23	2.9	72	3.5
	III	July 27	75	--	36	3.7	19	2.8	13	3.4	68	3.4
		July 28	--	75	28	2.5	28	2.1	16	1.9	72	2.2
	IV	July 29	69	--	25	4.3	18	4.5	13	4.1	56	4.3
		July 30	--	66	25	2.0	19	2.7	13	2.6	57	2.4
	V	August 3	60	--	29	2.0	19	3.0	1	2.5	49	2.4
		August 4	--	38	18	3.1	14	3.5	1	2.0	33	3.3

[1] The total number observed may exceed the number tagged. See text (p. 132) for explanation.

percentage varied from 40.1 to 62.8 in 1964 and from 44.2 to 61.8 in 1965. For chinook salmon, the range was 61.5 to 69.0% in 1965, the only year in which adequate data were obtained.

Travel Time from Release to Observation in Fish Ladders

Travel time by date of release, release location, and ladder for the 1964 and 1965 experiments are presented in Table 5. Following analysis of the 1964 data, we will examine the 1965 experiments (p. 135).

Analysis of variance tests of the hypothesis of no difference in travel time between left- and right-bank releases (all ladders combined) are given in Table 6. Because there were no releases from the right bank in period IV, the test compares the two left-bank releases. Within-release group variances were pooled to form an overall pooled estimate of the variance with 883 degrees of freedom. Because the mean travel times did not differ significantly between the July 15 and 16 left-bank releases, these releases were combined. The July 21 and 23 right-bank releases were similarly tested and combined. Note that in periods I to III, travel times for the left-bank releases were significantly less than

TABLE 6.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and released on the left bank below Rock Island Dam in 1964, traveled over the Rock Island Dam fish ladders equally as fast as fish released on the right bank; the testing period IV involves two left-bank releases.

Period	Release locations compared	Mean travel time in half-days, all ladders combined		F-statistics[1] (1 and 883 df)
		Left bank	Right bank	
I	Left vs. right	2.331	5.787	72.95 **
II	Left vs. right	3.394	4.617	8.71 **
III	Left vs. right	1.746	4.619	69.38 **
IV	Left (July 31) vs. Left (Aug. 3)	2.651 4.350	--	14.55 **
V	Left vs. right	4.628	3.604	3.11 N.S.

[1] ** = Highly significant at the 0.01 level, reject hypothesis of equal travel times, and conclude that travel time was significantly less for fish released from one bank than for those released on the other bank.
N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.

for the right-bank releases. In period IV when both releases were from the left bank, the travel time of fish released on August 3 was significantly higher than that of fish released on July 31. Differences were not significant in period V when fish were released from both left and right banks.

There is little doubt then that in periods I to III (when the spill pattern recommended by the study group was in operation), fish released from the left bank were finding the ladders and traveling over the dam faster than those released on the right bank. During the last two periods (V and VI), the flows were intentionally switched from the center to the right and back again. The effects of this change on fish passage are discussed in greater detail in a later section.

Further examination of Table 5 reveals two additional characteristics about the movement of tagged sockeye salmon over Rock Island Dam in 1964. First is the consistency of the relative passage times between ladders for fish from a given tag release. This means that regardless of how rapidly or slowly fish from a particular release moved, they did so more or less uniformly at all three ladders. Spring chinook salmon (Table 2) varied much more than did the sockeye in this respect. Second, in five of six comparisons fish released on the left bank negotiated the right-bank fish ladder faster than did fish released on the right bank. Considered jointly, these two features suggest that sockeye were capable of rapid lateral movement in the area downstream from the dam and that the passage of fish released on the right bank was somehow delayed whether they chose the left, center, or even the adjacent right-bank ladder.

Table 7 depicts the travel times by period and ladder, ignoring release sites. Corresponding statistical tests of the hypothesis of no difference in travel times between the right and center and between right and left fish ladders are included. For these tests, a pooled estimate of the error variance with 880 degrees of freedom was computed from within-ladder variances for the 15 groups. Because we tested left versus right and center versus right ladders simultaneously, using the same within-period data, we modified the *t*-test to control the type I error according to the method suggested by Dunn (1961).

Only one difference is significant. In period III, the mean passage time through the center ladder was less than through the right ladder. In general, however, passage time does not appear to be influenced by the ladder chosen.

Analysis of variance tests of the hypothesis of no difference in travel time between fish released on the right and left banks (all ladders combined) in 1965 are presented in Table 8. The conclusions from these tests are mixed. Fish traveled over the dam faster from the left-bank release site than from the right-bank release

TABLE 7.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and relased below Rock Island Dam in 1964, traveled over the right fish ladder at Rock Island Dam equally as fast as those traveling over the left and center ladders.

Period	Ladders compared	Mean travel time in half-days, release areas combined			*t*-statistics[1]	Degrees of freedom
		Left ladder	Center ladder	Right ladder		
I	Left vs. right	4.018	--	3.530	0.981 N.S.	(1, 159)
	Center vs. right	--	3.358	3.530	−0.329 N.S.	(1, 125)
II	Left vs. right	4.453	--	3.887	0.967 N.S.	(1, 187)
	Center vs. right	--	3.324	3.887	−0.893 N.S.	(1, 89)
III	Left vs. right	2.989	--	3.874	−1.494 N.S.	(1, 129)
	Center vs. right	--	2.014	3.874	−3.321 *	(1, 73)
IV	Left vs. right	3.042	--	4.399	−2.043 N.S.	(1, 117)
	Center vs. right	--	3.155	4.399	−1.461 N.S.	(1, 52)
V	Left vs. right	4.547	--	4.211	0.434 N.S.	(1, 108)
	Center vs. right	--	3.132	4.211	−1.215 N.S.	(1, 48)

[1] N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.
* = Significant at the 0.05 level, reject hypothesis of equal travel times, and conclude that travel time through the center ladder was significantly less than through the right ladder.

TABLE 8.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and released on the left bank below Rock Island Dam in 1965, traveled over the Rock Island Dam fish ladders equally as fast as fish released on the right bank.

Period	Mean travel time in half-days, all ladders combined		*F*-statistics[1] (1 and 613 df)
	Left-bank releases	Right-bank releases	
I	2.943	3.674	3.239 N.S.
II	4.589	3.543	4.915 *
III	3.374	2.182	12.867 **
IV	2.363	4.319	25.511 **
V	2.368	3.251	3.841 *

[1] N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.
* = Significant at the 0.05 level, reject hypothesis of equal travel times, and conclude that travel time for fish released on one bank was significantly less than for fish released on the other bank.
** = Significant at the 0.01 level, reject hypothesis, and conclude as above.

site in period I but not significantly so. In periods II and III, fish released on the right bank moved over the dam significantly faster than their left-bank counterparts. In periods IV and V, statistically significant differences were found only in the other direction, e.g., left-bank releases were faster than right-bank releases.

Thus, there is no clear superiority of one release location over the other. The effect of release location on relative and absolute travel times changed from period to period. In contrast, tagged sockeye salmon released from the left-bank site in 1964, before the spill was intentionally modified, moved past the dam faster than their right-bank counterparts. The main difference between the 2 years seems to be the decreased passage time for the right-bank releases of 1965 which, for every comparable period, moved over the dam faster than their 1964 counterparts.

Overall travel times (3.6 half-days in 1964 and 3.2 half-days in 1965) did not differ significantly despite the better performance by the right-bank releases.

Next, it is appropriate to examine the effect of ladder choice on mean travel time in 1965 by period and with release areas pooled. The basic data and the corresponding tests of significance are given in Table 9. No significant differences were found. Ladder choice did not appear to influence travel time. The same result was noted in 1964.

SPILL PATTERN MANIPULATION

On August 3, 4, and 5, 1964, spill was shifted from gates adjacent to the center ladder to the gate on the far right side of the dam. During this 3-day period, two groups of tagged fish (August 3 and 5) were released from the left bank and one (August 4) from the right bank. We will consider the left-bank releases first. The release of August 3 was subjected to 3 days of the modified spill condition, whereas the release of August 5 was subjected to 1 day of the same condition. The left-bank release of July 31 provided a crude "control" (no effect of modified

TABLE 9.—Analysis of variance tests of the hypothesis that sockeye salmon, tagged and released below Rock Island Dam in 1965, traveled over the right fish ladder at Rock Island Dam equally as fast as those using the left and center ladders.

Period	Ladders compared	Mean travel time in half-days, release areas combined			*F*-statistics[1]	Degrees of freedom
		Left ladder	Center ladder	Right ladder		
I	Right vs. left	3.642	--	2.868	3.051 N.S.	(1, 117)
	Right vs. center	--	2.906	2.868	0.004 N.S.	(1, 58)
II	Right vs. left	4.354	--	3.639	1.903 N.S.	(1, 137)
	Right vs. center	--	3.577	3.639	0.006 N.S.	(1, 56)
III	Right vs. left	3.096	--	2.502	1.766 N.S.	(1, 91)
	Right vs. center	--	2.340	2.502	0.155 N.S.	(1, 74)
IV	Right vs. left	2.946	--	3.288	0.402 N.S.	(1, 74)
	Right vs. center	--	3.464	3.288	0.080 N.S.	(1, 71)
V	Right vs. left	2.400	--	2.236	0.019 N.S.	(1, 47)
	Right vs. center	--	3.201	2.236	0.472 N.S.	(1, 33)

[1] N.S. = Not significant at the 0.05 level, accept hypothesis of equal travel times.

spill) for the two "experimental" releases on August 3 and 5.

The percentages of the tagged fish observed in the right ladder were 15.9, 23.8, and 31.9 for the releases of July 31 (0-day modified spill), August 3 (3-day modified spill), and August 5 (1-day modified spill), respectively. Comparable percentages were 19.5, 15.9, and 12.8 for the center ladder and 64.6, 60.3, and 55.3 for the left ladder. Travel times for the three releases averaged 2.7, 4.4, and 3.6 half-days respectively. Thus, it appears that spilling from the right side tended to attract fish released on the left bank to the right ladder but at the expense of increasing overall travel time.

The change in the spill pattern did not have a significant effect on tagged fish released on the right bank. For the July 30 "control" release, mean travel time was 4.6 half-days; for the August 4 "experimental" release it was 4.6 half-days. Slightly more fish from the August 4 release (19.5%) were attracted to the right ladder than from the July 30 release (12.6%).

Most striking is the similarity between the left-bank release of August 3 and the right-bank release of August 4. The percentages of tagged fish using various ladders for the releases of August 3 and 4 were: (see Table 5) left, 60.3 and 64.6; center, 15.9 and 15.9; and right, 23.8 and 19.5. Overall travel times were 4.4 and 4.6 half-days. Travel times by ladder were similar —4.4 and 4.8 half-days for the left, 2.8 and 3.3 for the center, and 5.6 and 5.6 for the right ladder.

In summary, the departure from the basic spill pattern tended to attract fish to the right-bank ladder, especially those released on the left bank and in so doing, increased the overall travel time. These experiments support the efficacy of the basic spill pattern as compared to the other pattern tested.

COMPARISON OF PREENCROACHMENT AND POSTENCROACHMENT TAGGING STUDIES

The effect of the encroachment of Wanapum Reservoir on fish passage at Rock Island Dam is best measured by comparing the results of the pre- and postencroachment tagging studies. We shall consider spring chinook salmon first, followed by sockeye salmon. Three measurements—percentage observed, distribution by ladder, and travel time—provide the basis of our analysis.

SPRING CHINOOK SALMON

The results of the 1954 and 1955 tagging studies with spring chinook salmon are presented in Tables 10 and 11. Comparable data for 1964 and 1965 are in Table 2.

Percentage Observed

The overall percentages of tagged spring chinook salmon observed passing Rock Island Dam were 38.7 and 59.9 in 1954 and 1955; they were 90.3 and 91.6 in 1964 and 1965. Although some of the significant increase may represent better tag retention or increased survival brought about by improved conditions for fish passage during the postencroachment study, it is likely that the precautions we took to improve the tag observations also were important.

It is interesting to note that the greatest increase occurred for fish released from the right-bank site. In 1954 and 1955, sightings from right-bank releases were only 37.5 and 51.9%, whereas in the postencroachment years—1964 and 1965—they were 81.1 and 94.9%. Few fish were released on the left bank in 1954, but the increase in the percentage of tagged fish observed for the other years (from 77.6 in 1955 to 95.5 and 88.4 in 1964 and 1965) while significant, is not as dramatic as for the right-bank releases.

Distribution by Ladder

The percentages of tagged spring chinook salmon in the left-bank fish ladder were 61.7, 74.5, 46.2, and 66.3 in 1954, 1955, 1964, and 1965, respectively. For the right ladder the percentages were 25.0, 16.0, 21.5, and 15.4 for the 4 years, respectively. This means that 13.3% used the center ladder in 1954, 9.6% in 1955, 32.3% in 1964, and 18.2% in 1965. Thus, there was no

TABLE 10.—Tag release and observation data for spring chinook salmon seen passing over fish ladders at Rock Island Dam, 1954 and 1955.[1]

Date	Tagging location	Number of fish tagged and released	Number of tagged fish observed			
			Left ladder	Center ladder	Right ladder	Total
1954						
June 23-25	Right bank	26	6	3	7	16
June 29-July 2	Right bank	36	5	2	2	9
July 7-9	Right bank	57	7	1	5	13
July 13	Right bank	26	15	2	0	17
July 16-22	Left bank	3	3	0	0	3
July 29-30	Right bank	7	1	0	1	2
1955						
June 7-9	Left bank	8	3	0	1	4
	Right bank	14	7	1	1	9
June 14-15	Right bank	13	7	1	2	10
June 17-21	Left bank	9	10	0	2	12
	Right bank	19	6	1	2	9
June 28-29	Right bank	15	10	0	0	10
June 30-July 1	Right bank	19	3	2	2	7
July 5-6	Left bank	17	8	3	1	12
July 7-8	Right bank	43	16	1	4	21

[1] The total number observed may exceed the number tagged. See text (p. 132) for explanation.

TABLE 11.—Travel time of tagged spring chinook salmon from tagging areas below Rock Island Dam to the Rock Island fish ladders, 1954 and 1955.

Date	Tagging location	Mean travel time in half-days, all ladders combined
1954		
June 23-25	Right bank	12.3
June 29-July 2	Right bank	7.4
July 7-9	Right bank	14.9
July 13	Right bank	13.8
July 16-22	Left bank	15.8
July 29-30	Right bank	10.6
1955		
June 7-9	Left bank	6.5
	Right bank	19.4
June 14-15	Right bank	12.4
June 17-21	Left bank	24.2
	Right bank	21.8
June 28-29	Left bank	20.3
June 30-July 1	Right bank	9.2
July 5-6	Left bank	19.6
July 7-8	Right bank	12.8

marked and repeatable difference in distribution by ladder between the postencroachment years, 1964 and 1965, and the preencroachment years, 1954 and 1955. The center ladder took a disproportionate share of the fish in 1964 (at the expense of the left ladder), but this was less pronounced in 1965.

Travel Time from Release to Observation in Fish Ladders

Apparently no large-scale mortalities and no great losses of tags were caused by encroachment (these assumptions are supported by the high percentages of tagged fish subsequently seen passing Rock Island Dam). The overall effect of encroachment is then best measured by comparing the travel times between the pre- and postencroachment tagging studies. Although we have already shown that the 1965 travel time (5.8 half-days) was significantly less than the 1964 travel time (9.0 half-days), this difference does not overshadow the fact that both values are well below the comparable figures (12.4 and 16.0 half-days) for 1954 and 1955, respectively. We can only conclude that travel time of spring chinook has decreased markedly since encroachment.

SOCKEYE SALMON

Results of the 1954 and 1955 tagging studies with sockeye salmon are given in Table 12. Comparable data for 1964 and 1965 are presented in Table 5.

TABLE 12.—Tag releases, tag observations, and travel times for sockeye salmon seen passing over fish ladders at Rock Island Dam, 1954 and 1955.

Period	Date	Tagging location	Number of fish tagged and released	Number of tagged fish observed[1]	Mean travel time in half-days
1954					
I	July 7-8	Right bank	22	22	23.3
II	July 16, 20	Left bank	119	168	12.5
	July 21-22	Right bank	155	151	10.1
III	July 22-23	Left bank	272	196	8.4
	July 27-29	Right bank	146	75	7.7
IV	July 28-30	Left bank	246	111	7.3
	August 3	Right bank	89	80	6.6
V	August 6-12	Left bank	174	128	4.8
	August 5-12	Right bank	262	245	6.4
1955					
I	July 19-20	Right bank	123	118	7.3
II	July 21	Left bank	59	46	7.0
	July 22	Right bank	46	6	14.9
III	July 26-29	Left bank	298	224	7.0
	July 26-28	Right bank	227	151	5.2
IV	August 2-3	Left bank	129	119	7.1
	August 2	Right bank	24	12	3.8
V	August 5-10	Left bank	93	38	7.1
	August 4-11	Right bank	177	79	7.5

[1] The number observed may exceed the number tagged. See text (p. 132) for explanation.

Percentage Observed

The overall percentages of tagged sockeye salmon observed passing Rock Island Dam in 1964 and 1965 (94.1 and 91.8, respectively) were significantly higher than those recorded in 1954 and 1955 (79.2 and 67.4). A similar change was noted for chinook salmon. As we mentioned earlier in discussing the results with chinook salmon, two factors—increased tag retention and improved facilities for observing and reporting tagged fish—probably contributed to the increased percentages of tagged fish that were observed. Unlike chinook salmon, for which a greater part of the increased percentage of fish sighted could be attributed to fish released on the right bank, the improvement in sockeye salmon was of the same magnitude for releases made on both banks.

Distribution by Ladder

Percentages of tagged sockeye salmon in the left ladder were 55.3, 64.3, 55.6, and 53.1 in 1954, 1955, 1964, and 1965, respectively. For the right ladder, the percentages were 13.2, 12.4, 23.7, and 23.3; for the center ladder they were 31.5, 23.3, 20.7, and 23.6. As with chinook salmon then, the distribution of tagged sockeye salmon by ladder in postencroachment years, 1964 and 1965, did not differ significantly or at least consistently so from that observed in preencroachment years, 1954 and 1955.

Travel Time from Release to Observation in Fish Ladders

Comparisons of the mean travel times by period and area of release for 1954 versus 1964 and 1965 and for 1955 versus 1964 and 1965 are presented in Figure 5. On only 1 of 34 occasions was the travel time in the preencroachment tagging year less than for the corresponding postencroachment tagging year. The difference was not significant.

As with chinook salmon then, we found the time required by tagged sockeye salmon to pass the fish ladders at Rock Island Dam was considerably less after the onset of encroachment than before.

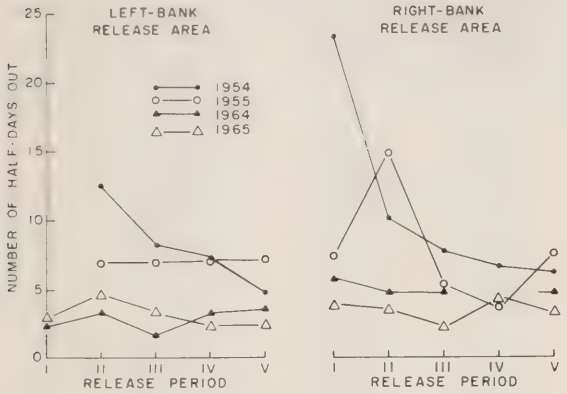

FIGURE 5.—Time required for tagged sockeye salmon to move over the Rock Island Dam fish ladders from the tagging areas below the dam, 1954, 1955, 1964, and 1965.

SUMMARY AND CONCLUSIONS

The lower portions of the fish ladders at Rock Island Dam were flooded by the reservoir of Wanapum Dam. At the direction of the Federal Power Commission, the fish ladders were modified to maintain or enhance fish passage and a study was developed to evaluate the adequacy of the modifications.

In 1964 and 1965 over 2,000 spring chinook and sockeye salmon were tagged and released below Rock Island Dam; their subsequent movement over the fish ladders was noted. Three features—travel time, the percentage of tagged fish observed, and the distribution of tagged fish by ladder—were compared with data obtained in a similar tagging study in 1954 and 1955.

Results clearly indicate that the fish passage over Rock Island Dam was better in 1964 and 1965 than in 1954 and 1955. Travel times were significantly shorter and higher percentages of tagged fish were sighted passing over the ladders under postencroachment conditions.

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SCALE FEATURES OF SOCKEYE SALMON FROM ASIAN AND NORTH AMERICAN COASTAL REGIONS

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ABSTRACT

Photographic plates of sections of sockeye salmon scales, with descriptions, and frequency tables of the number of circuli in the freshwater and first ocean zones illustrate the variations in scale features of fish over the range of the species in coastal regions of Asia and North America. Suggestions are also given for using these data to determine the geographical origin of sockeye salmon taken in offshore areas of the North Pacific Ocean and adjacent waters.

Sockeye salmon (*Oncorhynchus nerka*) are valuable food fish of the Bering Sea and the northern part of the North Pacific Ocean. They spawn in coastal streams of Asia and North America but spend a portion of their lives feeding in oceanic areas. Upon the onset of sexual maturity, they migrate from the ocean, enter their natal streams, spawn, and then die. Because sockeye return to natal streams to spawn, the species is divided into hundreds of individual populations (each from its own geographical area), which are self-reproducing units or "stocks."

A major goal in fisheries research and management of the sockeye salmon resource is to obtain enough spawning fish within each stream to provide the maximum catch to the fishery and to insure the perpetuation of each stock. This goal is difficult to attain in fishing areas where management agencies are uncertain of the geographic area of origin of the stocks of fish that are being caught. Consequently, methods for determining the area of origin of sockeye salmon taken beyond their natal streams are needed.

A number of methods have been used to determine the area of origin of sockeye salmon taken in offshore and coastal areas. These include morphological studies (Fukuhara et al., 1962; Landrum and Dark, 1968), parasitological studies (Margolis, 1963), serological studies (Ridgway, Klontz, and Matsumoto, 1962), tagging studies (Hartt, 1962, 1966; Kondo et al., 1965), and scale studies (Krogius, 1958; Kubo, 1958[2]; Kubo and Kosaka, 1959[3]; Henry, 1961; Mosher, Anas, and Liscom, 1961; and Mosher, 1963, 1968). Scale studies have become one of the most popular and successful methods; scale features, for example, are routinely used by investigators of the International Pacific Salmon Fisheries Commission as one element in a technique to determine the natal streams of sockeye taken near the mouth of the Fraser River and are also routinely used by investigators of the National Marine Fisheries Service (NMFS, formerly the Bureau of Commercial Fisheries) to determine continent of origin of sockeye salmon taken in the Bering Sea and the central North Pacific Ocean.

No detailed information, however, has been published on the variations in scale features among fish from different spawning regions along the Asian and North American coasts. Krogius (1958) specifically mentioned the need for an atlas illustrating scales from different

[1] National Marine Fisheries Service, Northwest Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98102.

[2] Kubo, T. 1958. Study of sockeye salmon stocks by means of the growth pattern of scales (preliminary report). Fac. Fish., Hokkaido Univ. (Hakodate). Part I - 15 p. of Japanese text; Part II - 2 pl., 16 fig. in English. (Transl. of Part I, Int. North Pac. Fish. Comm. Doc. 206), 9 p. (Processed.)

[3] Kubo, T., and J. Kosaka. 1959. A study of 5_3 age group red salmon stocks by scale growth formula [in Japanese with English abst., headings, tables, and fig. legends.] Suisan cho (Fisheries Agency of Japan), (Int. North Pac. Fish. Comm. Doc. 326), 27 p. (Processed.)

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areas and included in her paper were many pictures of scales of sockeye salmon of Asian stocks. A photographic atlas of sockeye salmon scales (Mosher, 1968) was the first step in determining racial origins, and it should be available for reference when the present paper is studied.

The purpose of this paper is to show variations in age and scale characteristics among adult fish from various coastal areas over the range of the species so that workers planning to collect and analyze scale data to determine origin of sockeye taken at sea and in coastal waters are informed about scale features that are linked to various geographic localities.

This report consists of two principal parts. The first comprises (1) photographs of sections of scales of adult sockeye salmon, as plates, for each freshwater age group from various areas over the range of the species; (2) frequency tables of the number of circuli in the freshwater and first ocean zones for fish taken from the various areas; and (3) descriptions of the scales of sockeye salmon from the various areas. The second part is concerned with the selection of scale features for the determination of the origin of fish taken in offshore waters.

METHODS AND MATERIALS

In the preparation of this paper I was concerned with (1) the selection of scale samples of fish from various geographical areas, (2) the selection of scale features that are linked to various stocks or geographical areas, and (3) the method of preparation of plates from photographs of selected sockeye scales. I have discussed each of these items separately.

SELECTION OF SCALE SAMPLES OF FISH FROM VARIOUS GEOGRAPHICAL AREAS

An important consideration in deciding which stocks of sockeye salmon to include in this paper was the relative number of fish produced in the various localities over the range of the species shown in Figure 1. Study of catch data seems to be the best way to determine the most abundant stocks because the catch is roughly proportional to the production of fish in an area. Table 1 shows the average catch for the 3 years, 1966-68, the statistics for which are complete for Asia

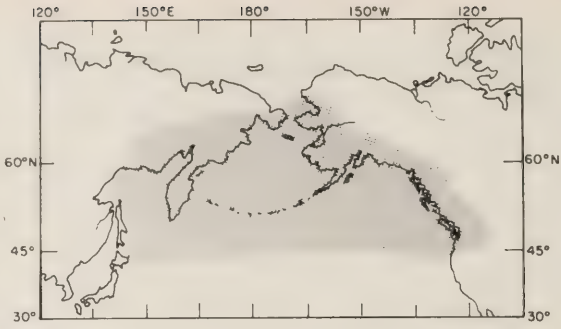


FIGURE 1.—Approximate range of sockeye salmon in and around the North Pacific Ocean and adjacent seas. The distribution in the northern Bering and Chukchi Seas was estimated to include the northernmost known spawning streams on both continents. Sockeye salmon may be found in many streams within the range shown, but in only a few streams in some areas. Atkinson et al. (1967) shows detailed maps of streams where sockeye salmon have been known in the United States. The distribution at sea varies within and between years, depending on many factors, Manzer et al. (1965), Hartt (1962, 1966), and Kondo et al. (1965). In addition to the above references, Hanamura (1966, 1967) and Aro and Shepard (1967) were also sources of data for this figure.

TABLE 1.—Sockeye salmon catch, average of 1966-68.

Area	Thousands of fish	Metric tons
Total all areas	27,297.2	70,387.0
Asia	9,512.6	20,972.6
Japan[1]	8,527.0	17,988.6
USSR	985.6	2,984.0
North America	17,784.6	49,414.4
Canada (British Columbia)	5,676.4	
United States	12,108.2	
North of Bristol Bay	2.8	
Bristol Bay[2]	5,715.0	
Alaska Peninsula[3]	1,625.5	
Cook Inlet	1,465.7	
Copper River area[4]	832.2	
Southeastern Alaska[5]	952.1	
Washington and Oregon[6]	1,514.9	

[1] Japan has no stocks of sockeye salmon.
[2] Includes north side of Alaska Peninsula.
[3] Includes Aleutian Islands, south side of Alaska Peninsula, Chignik, and Kodiak Island.
[4] Includes Resurrection Bay, Prince William Sound, Copper and Bering Rivers.
[5] Includes Yakutat.
[6] Includes the Columbia River (32.2 thousand fish).
Source of data: International North Pacific Fisheries Commission, 1966, 1967, and 1968; and supplemental catch statistics supplied to the INPFC by the USSR.

and North America from International North Pacific Fisheries Commission (INPFC) sources. The approximate ranking on each continent of the importance of the coastal areas is as follows:

Asia (from Hanamura, 1966 and Krogius, 1958)		*North America (from catch data of Table 1)*	
Ozernaya River	1	Bristol Bay	1
Kamchatka River	2	British Columbia	2
Bolshaya River	3	Alaska Peninsula	3
Paratunka River	4	Washington and Oregon	4
Apuka River	5	Cook Inlet	5
Okhota and Kukhtuy Rivers	6	Southeastern Alaska	6
		Copper River area	7
		Columbia River	8
		North of Bristol Bay	9

The abundance and catch of sockeye salmon in most areas can fluctuate widely between years, however. Some of these variations in catch are revealed in Appendix Table 1 of the catch of the 5 years, 1964-68, which series includes one high production year in Bristol Bay—1965.

The distribution of spawning streams in Asia extends from approximately lat 66° N near the Anadyr River southward to the tip of the Kamchatka Peninsula and the Kurile Islands, and westward to the Okhota and Kukhtuy Rivers on the northern coast of the Okhotsk Sea (Hanamura, 1966, 1967). Berg (1948) indicated that the species was very rare in northern Hokkaido Island. Krogius and Krokhin (1956) concluded that approximately 90% of the total sockeye catch along the Far Eastern Coast of the USSR was produced in the Ozernaya and Kamchatka Rivers of the Kamchatka Peninsula.

The distribution of North American spawning streams extends from the Noatak River of Kotzebue Sound in Northern Alaska, southward to the Columbia River of Oregon and Washington (Aro and Shepard, 1967; Atkinson et al., 1967). The streams can be conveniently grouped into three major geographical areas for study: (1) the Columbia River to and including British Columbia: (2) Bristol Bay, Alaska, and areas north of Bristol Bay; and (3) the area between Bristol Bay and British Columbia. In many years each area contributes about one-third of the North American catch. Normally, the catch of sockeye salmon north of Bristol Bay is insignificant in relation to the number of fish taken in the Bay, but consumption and barter of salmon is substantial, especially by residents along the Kuskokwim River.

Thus, plates of representative scales of fish from southern Kamchatka, Bristol Bay, and the areas north of Bristol Bay, central and southeastern Alaska, British Columbia, and the Columbia River (the coastal areas listed in Table 1) are included in the first part of this paper.

The scale samples used in a previous study (Mosher, 1968) with a few samples, which have recently become available from additional areas, were used for this study.[4] The areas from which these samples were collected are listed in Table 2. Figure 2 shows the approximate location of the areas mentioned in the text and on the plates.

SELECTION OF SCALE FEATURES LINKED TO VARIOUS STOCKS OR AREAS

My previous paper (Mosher, 1968) shows in detail the features of sockeye salmon scales and the range of variations in many characters. This paper continues the study of sockeye salmon scales to show the relation of many of the variations to locality and how these variations in scale characters can be used to identify the mainland origin of sockeye salmon taken in offshore waters.

A number of age groups have been found in all populations of sockeye salmon that have been studied. These age groups are based on the number of years the fish lived in fresh water and in the ocean. Over the geographical range of the species, individuals with scales showing freshwater ages from 0. to 4., ocean ages from .1 to .4, and total ages of 0.1 to

[4] Contributions of the following agencies to the salmon scale sampling program are gratefully acknowledged: The Alaska Department of Fish and Game, Juneau, Alaska; the Fisheries Research Board of Canada, Nanaimo, B.C.; the Fisheries Agency of Japan, Tokyo, Japan; and the Fish Commission of Oregon, Portland, Oreg. In addition, special thanks are given to Dr. I. Lagunov of the Pacific Institute of Fisheries Research and Oceanography (TINRO), Petropavlovsk, Kamchatka, USSR, who kindly supplied a series of samples from USSR streams.

TABLE 2.—Geographical areas where scales were taken from sockeye salmon. (Scales are available at the National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Wash.)

Asia
- 1. Kamchatka River
- 2. Paratunka River
  - A. Dalnee Lake
  - B. Blizhnee Lake
- 3. Bolshaya River
- 4. Ozernaya River
- 5. Okhtosk Sea
- 6. North Pacific Ocean and Bering Sea from areas near the Kamchatka Peninsula

North America
- 7. Nome area
  - A. Salmon Lake
  - B. Unalakleet River
- 8. Kuskokwim River
- 9. Bristol Bay
  - A. Togiak River
  - B. Nushagak-Wood River System[1]
  - C. Kvichak River[1]
  - D. Naknek River[1]
    - (1) Brooks Lake
    - (2) Branch River
  - E. Egegik River[1]
  - F. Ugashik River[1]
  - G. Bear River
- 10. Aleutian Islands
  - A. Attu
  - B. Adak
  - C. Unalaska
- 11. Alaska Peninsula area[2]
  - A. King Cove
  - B. Chignik
  - C. Kodiak Island
    - (1) Karluk
    - (2) Red River
    - (3) Frazer River
- 12. Cook Inlet area[2]
  - A. Cook Inlet Fishery
  - B. Kenai River
  - C. Susitna River
    - (1) Fish Creek
    - (2) Judd Lake
    - (3) Alexander Creek
  - D. Kasilof River
  - E. Fish Creek, Knik Arm, Kenai Peninsula
  - F. Skilak Lake
  - G. Tustamina Lake (Bear Creek)
  - H. Upper Russian Lake
- 13. Copper River[2]
  - A. Haley Creek
- 14. Yakutat
  - A. Situk River
- 15. Petersburg area[2]
  - A. Kasheets
  - B. Stikine River
  - C. Salmon Bay
  - D. Tahlton Lake
  - E. Red Bay
  - F. Port Houghton
- 16. Ketchikan area[2]
  - A. Portland Canal
  - B. Moira Sound
    - (1) North Arm
    - (2) Kegan Creek
  - C. Karta Bay
  - D. Dolomi Lake and Stream
  - E. Hugh Smith Stream
  - F. Clarence Strait
  - G. Eek Bay
  - H. Hetta Bay
  - I. Nicholas Bay
  - J. Nichols Bay
  - K. Klawock Creek
  - L. Klakas Lake
  - M. Deweyville
- 17. British Columbia
  - A. Nass River
  - B. Skeena River
  - C. Rivers Inlet
  - D. Smith Inlet
  - E. Alert Bay
  - F. Nimpkish River
  - G. Fraser River
- 18. Columbia River
  - A. Main stem
  - B. Wenatchee River
  - C. Okanogan River

[1] Samples from the five major Bristol Bay rivers were taken each year since 1954. There are samples for most other areas for a number of years, but there is only one sample for some of the less important areas.
[2] Additional samples were taken, but numbers of scales were small.

[5]3.4 occur, but in most localities most fish are in age groups 1.2, 1.3, 2.2, and 2.3.

The number of years spent in fresh water varies within and between many spawning areas and influences many of the scale characters (Mosher, 1963, 1968). Only a few adult fish of age 0. or 4. are found, some fish of age 3. are found in a few areas, but fish of age 1. and 2. are present in substantial numbers in most areas. Table 3 shows the percentage freshwater age composition of sockeye salmon in stream samples (except as noted) from areas around the North Pacific Ocean available at the NMFS Northwest Fisheries Center.

Many features of sockeye salmon scales can be used in racial studies. Scientists at the NMFS Northwest Fisheries Center in Seattle have examined about 50 different features such as counts of circuli, measurement of zones and portions of zones, and various ratios based on these counts and measurements; but only scale characteristics with the greatest difference between Kamchatkan and Bristol Bay stocks have been described in our publications (Mosher et al., 1961; Mosher, 1963, 1968; Anas, 1964; Anas and Murai, 1969). In all of our studies—published and unpublished—the best features for racial studies have been in the freshwater and first ocean zones of the scale.

Because of the large number of Asian and North American spawning areas and the large number of age groups in some areas, it is evident that space is not available for examples of scales representative of each area and age group over the geographic range of the species. Scales from numerous areas are similar in many characters; consequently I will group together scales from fish of more than one stock or spawning area that have a relatively similar appearance.

The number of circuli in the freshwater and first ocean zones (counted as indicated on p. 36

[5] Age designation follows the European system, Koo (1962a): the number of winters the fish spent in fresh water since hatching, a decimal point, and the number of winters the fish spent in the ocean (see Mosher, 1968, p. 259 and 262).

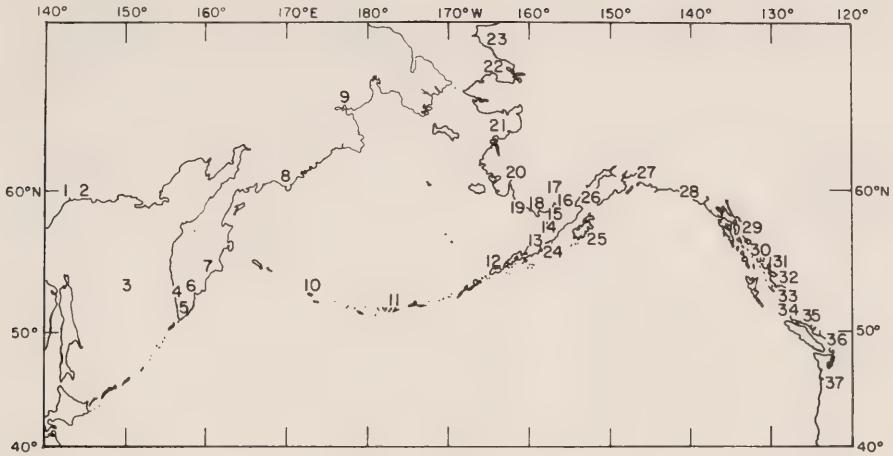


FIGURE 2.—Approximate location of areas mentioned in the text and on the plates.

1. Okhota River
2. Kukhtuy River
3. Okhotsk Sea
4. Bolshaya River
5. Ozernaya River
6. Paratunka River (Dalnee and Blizhnee Lakes)
7. Kamchatka River
8. Apuka River
9. Anadyr River
10. Attu Island
11. Adak Island
12. Unalaska Island
13. Bear and Sandy Rivers
14. Ugashik River
15. Egegik River
16. Naknek River
17. Kvichak River
18. Nushagak-Wood River system
19. Togiak Bay
20. Kuskokwim River
21. Norton Sound-Yukon River
22. Kotzebue Sound
23. Noatak River
24. Chignik Bay
25. Kodiak Island
26. Cook Inlet
27. Copper River area
28. Yakutat Bay
29. Petersburg area
30. Ketchikan area
31. Nass River
32. Skeena River
33. Rivers Inlet
34. Smith Inlet
35. Nimpkish River
36. Fraser River
37. Columbia River

and 37 of Mosher, 1963) are shown for the various areas as frequency tabulations in Tables 4 and 5 for the age 1. fish; in Tables 6 and 7 for the age 2. fish; and in Table 8 for the age 3. fish. Inspection of Tables 4 and 6 shows that the mean number of circuli in the freshwater zone varies among some geographical areas, but that in the first ocean zone (Tables 5 and 7) there is a cline in number of circuli from least in the Adak Island fish to most in the central British Columbia areas of Rivers and Smith Inlets and the Nimpkish River. A decrease in the mean number of circuli among stocks from central British Columbia southward to the Columbia River is also found. The Asian fish and those north of Bristol Bay have slightly more circuli, on the average, than those of Adak Island and Bristol Bay.

The scales from sockeye taken from certain geographic areas have similar frequency distributions of circuli in the freshwater or first ocean zone. These similarities are the basis for dividing the coast of North America into certain broad areas. When I discuss the various geographic areas, reference will be made to the appropriate frequency table.

PREPARATION OF PLATES

The scale plates for the report were made as follows: (1) The scale images produced by a scale projector like the one I described (Mosher, 1950), at 82× magnification, were photographed with a 35-mm single lens reflex camera on medium speed, fine grained film and processed to accentuate the contrast by minimum exposure

TABLE 3.—Percentage freshwater age composition of samples of sockeye salmon from geographical areas of the North Pacific Ocean from those listed in Table 2.

Locality	Year[1]	Freshwater age					Number in sample
		0.	1.	2.	3.	4.	
				Percent			
Asia[2]							
Ozernaya R.	1959	--	0.8	53.3	45.1	0.8	124
Bolshaya R.	1964	1.2	94.1	3.5	1.2	--	84
Kamchatka R.	1964	2.2	90.2	6.5	1.1	--	92
Paratunka R.:							
Dalnee Lake	1964	--	2.9	44.3	52.8	--	70
Blizhnee Lake	1958	--	0.6	78.5	20.3	0.6	172
Okhotsk Sea	1957	--	51.5	42.1	6.4	--	501
Off S.E. Kamchatka	1965	--	21.9	59.2	16.9	2.0	201
North America:							
Kuskokwim	1959	--	70.5	28.7	0.8	--	122
Bristol Bay:							
Ugashik R.	1966	--	39.6	60.4	--	--	318
Egegik R.	1966	--	5.9	86.9	7.2	--	305
Naknek R.	1966	--	32.0	67.2	0.8	--	356
Kvichak R.	1966	--	4.0	95.7	0.3	--	351
Nushagak R.	1966	--	94.7	5.3	--	--	322
Togiak R.	1955	3.3	80.1	16.6	--	--	307
Bear R.	1959	--	1.6	95.0	3.4	--	119
Aleutian Islands:							
Attu Isl.	1956	1.3	38.8	52.9	6.6	0.4	227
Adak Isl.	1956	--	30.6	60.5	8.0	0.9	213
Unalaska Isl.	1956	--	38.9	37.5	22.9	0.7	144
Alaska Peninsula:							
King Cove	1957	--	45.7	52.7	1.6	--	182
Chignik R.	1957	--	40.0	59.3	1.7	--	175
Karluk R.	1959	--	--	48.1	47.2	4.7	106
Red River	1959	--	--	85.1	14.9	--	107
Cook Inlet	1959	--	83.9	16.1	--	--	118
Cook Inlet Fish Cr.	1959	--	98.3	1.7	--	--	120
Southeastern Alaska:							
Copper R.	1959	--	87.7	12.3	--	--	122
Yakutat R.	1958	--	31.5	65.6	2.9	--	105
Petersburg	1964	4.6	81.8	13.0	0.6	--	323
Ketchikan	1964	0.3	84.1	15.6	--	--	352
British Columbia:							
Nass R.	1964	--	35.0	65.0	--	--	320
Skeena R.	1964	--	98.7	1.3	--	--	297
Rivers Inlet	1961	--	98.0	2.0	--	--	248
Smith Inlet	1961	--	100.0	--	--	--	255
Nimpkish R.	1967	--	64.5	30.4	5.1	--	79
Fraser R.	1964	0.7	98.0	1.3	--	--	153
Columbia River	1964	0.2	88.1	11.7	--	--	416

[1] The year selected is the most complete for that area, is in a series with adjacent areas, or is the only year a sample is available in our series (Table 2).
[2] Historical data on age composition of samples from Ozernaya, Bolshaya, and Kamchatka Rivers, and Lake Dalnee for a number of years from 1931 to 1960 are available in Hanamura (1966).

and maximum development (Adams, 1952; Mortensen, 1947). (2) Positive prints of sections that showed the important features of the anterior field of the scales were made from these negatives on high contrast enlarging paper. (3) The positive prints of the scale sections were assembled by area groups on mounting sheets and photographed to provide the plates. The scales were all photographed at the same magnification. Consequently, the relative size of the scale features on the plates reflects the relative size of the scale features themselves.

As indicated in my previous paper (Mosher, 1968), the texture, contrast, and distinctness of circuli vary greatly both on individual scales and between the scales of the same and different fish. Some scales can be photographed to show the features clearly; other scales, especially from some localities with many closely spaced and broken circuli, do not provide clear photographs of all features.

TABLE 4.—Percentage frequency distribution[1] of circuli in the total freshwater zone from age 1. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska												British Columbia						
	Kamchatka River[2]	Bolshaya River[2]	Dalnee Lake[3]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[6]	Chignik[7]	Cook Inlet[8]	Fish Creek[7]	Copper River[9]	Yakutat[5]	Petersburg[2]	Ketchikan[2]	Nass River[8]	Skeena River[8]	Rivers Inlet[9]	Smith Inlet[9]	Nimpkish River[10]	Fraser River[9]	Columbia River[7]
											Percent											
5	1.9	1.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.5	--	--	--	--
6	5.6	6.5	--	--	--	--	--	--	--	--	--	1.1	--	2.2	0.5	--	--	1.9	1.0	--	--	--
7	7.4	12.0	--	--	--	0.7	--	--	--	0.5	--	3.8	0.5	6.5	1.5	--	--	4.8	4.5	--	--	--
8	9.6	14.7	--	0.4	--	2.8	--	--	--	1.5	--	4.7	3.1	11.2	2.5	--	--	10.5	8.5	0.5	--	--
9	13.3	16.4*	--	0.9	--	7.0	--	--	0.6	2.0	--	4.9	6.6	15.9*	2.5	0.5	--	18.3	12.5	0.9	--	--
10	16.7	14.0	--	1.3	--	13.0	--	--	2.8	2.0	--	6.7	9.2	15.9*	2.5	3.0	0.5	23.3*	20.0	3.9	--	--
1	18.2*	9.9	--	3.0	--	16.9*	--	--	6.0	4.0	--	9.6	11.2	12.5	7.0	5.5	2.5	20.0	23.5*	9.3	--	--
2	13.9	8.6	--	4.3	0.1	14.8*	--	--	8.5	10.5	--	14.2	12.8	10.8	14.5	4.5	6.5	11.7	15.5	9.8	0.6	0.3
3	7.4	6.2	--	3.0	1.9	9.5	--	--	12.5	18.5	--	16.9*	14.8	8.6	21.0	5.5	10.0	6.0	6.0	6.4	1.7	0.6
4	3.1	3.1	0.5	0.9	6.5	7.0	--	--	17.0*	20.5*	--	16.3	18.4*	6.5	22.5*	13.0	13.5	2.6	3.5	5.4	2.8	0.3
5	1.2	1.7	2.7	2.2	11.3	7.0	--	0.5	16.2	16.0	--	12.2	15.8	5.2	15.0	21.0*	21.0	0.5	3.5	4.9	5.6	0.6
6	1.2	1.4	5.5	7.8	15.1	5.6	--	3.7	11.1	11.5	--	5.8	6.1	3.0	6.0	21.0*	23.5*	--	1.5	3.4	10.1	1.8
7	0.6	1.4	5.5	12.4	18.6	3.5	0.8	7.9	8.0	7.5	--	2.3	1.0	1.3	2.0	13.5	15.0	--	--	4.9	14.6	2.1
8	--	1.0	7.3	19.8	19.5*	3.2	4.0	7.9	7.1	3.5	--	1.1	0.5	0.4	1.0	7.0	6.0	--	--	10.3	16.6*	4.3
9	--	0.7	14.1	22.8*	15.5	3.2	8.5	6.5	5.4	1.5	0.3	0.3	--	--	1.0	3.5	1.5	--	--	13.7*	13.5	10.1
20	--	0.7	17.7*	13.8	8.7	2.1	10.9	6.5	2.6	0.5	0.9	--	--	--	0.5	1.5	--	--	--	9.8	10.4	14.3
1	--	0.3	15.5	5.2	2.6	0.7	11.3	5.6	1.1	--	5.2	--	--	--	--	0.5	--	--	--	5.4	10.1	16.8
2	--	--	14.1	1.7	0.1	0.4	11.3	4.2	0.9	--	14.3	--	--	--	--	--	--	--	--	4.4	8.4	17.1*
3	--	--	11.4	--	--	0.7	11.7	5.1	0.3	--	21.0	--	--	--	--	--	--	--	--	2.5	4.5	14.3
4	--	--	4.1	--	--	0.7	12.5*	9.2	--	--	22.6*	--	--	--	--	--	--	--	--	0.9	1.1	10.7
5	--	--	0.5	--	--	0.7	10.5	13.0*	--	--	18.9	--	--	--	--	--	--	--	--	0.9	--	5.2
6	--	--	0.9	--	--	0.4	6.0	11.1	--	--	11.0	--	--	--	--	--	--	--	--	0.5	--	1.2
7	--	--	0.5	--	--	--	3.6	6.9	--	--	4.6	--	--	--	--	--	--	--	--	0.5	--	0.3
8	--	--	--	--	--	--	3.6	5.6	--	--	1.2	--	--	--	--	--	--	--	--	0.9	--	--
9	--	--	--	--	--	--	3.6	4.2	--	--	--	--	--	--	--	--	--	--	--	0.5	--	--
30	--	--	--	--	--	--	1.6	1.9	--	--	--	--	--	--	--	--	--	--	--	--	--	--
1	--	--	--	--	--	--	--	0.5	--	--	--	--	--	--	--	--	--	--	--	--	--	--
Number of fish	81	73	55	58	181	71	62	54	88	50	82	86	49	58	50	50	50	105	50	51	89	82

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1964.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956.
[7] 1963.
[8] 1965.
[9] 1961.
[10] 1967.
* Indicates modes.

TABLE 5.—Percentage frequency distribution[1] of circuli in the first ocean zone of age 1. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska												British Columbia						
	Kamchatka River[2]	Bolshaya River[2]	Dalnee Lake[3]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[6]	Chignik[7]	Cook Inlet[8]	Fish Creek[7]	Copper River[9]	Yakutat[9]	Petersburg[2]	Ketchikan[2]	Nass River[4]	Skeena River[4]	Rivers Inlet[10]	Smith Inlet[9]	Nimpkish River[10]	Fraser River[9]	Columbia River[7]
	Percent																					
10	--	--	--	--	--	--	0.1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
11	--	--	--	--	--	--	0.9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
2	--	--	--	--	--	--	2.7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
3	--	--	--	--	0.1	0.1	5.9	0.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--
4	--	--	--	--	0.4	0.4	10.0	1.2	--	--	--	--	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	1.1	0.8	12.6	3.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6	--	--	--	0.4	3.9	1.2	13.3*	5.4	--	--	--	--	--	--	--	--	--	--	--	--	--	--
7	--	0.3	1.4	2.2	8.6	2.6	13.2*	7.0	--	--	--	--	--	--	--	--	--	--	--	--	--	--
8	1.2	0.7	3.2	5.2	12.3	5.1	10.8	9.6	0.6	--	--	--	--	--	--	--	--	--	--	--	--	--
9	3.1	0.7	3.6	9.1	16.7	7.3	8.4	13.7	1.4	2.0	0.9	--	--	--	--	--	--	--	--	--	--	--
20	3.7	1.0	5.9	11.2	21.0*	12.6	7.4	14.8*	2.3	6.5	2.7	0.3	--	--	--	--	--	--	--	--	0.3	--
1	6.8	4.5	12.3	15.5	18.1	16.9*	5.8	11.2	4.5	11.0	5.5	0.9	--	1.3	--	0.5	--	--	--	--	0.6	0.9
2	12.3	12.3	19.1	21.1*	10.5	14.9	3.8	9.5	8.5	13.5	11.0	2.0	--	3.0	0.5	1.5	0.5	--	--	--	1.4	4.0
3	17.6	19.5	20.0*	17.2	5.0	13.2	2.3	8.9	14.2	17.0	17.4	4.1	1.0	2.5	2.0	3.0	3.0	--	--	--	5.1	7.3
4	20.7*	21.2*	15.5	10.3	1.9	11.5	1.5	6.4	17.3*	20.0*	18.9*	6.4	4.1	2.2	3.0	4.5	10.5	--	--	--	9.8	9.8
5	17.2	18.1	10.5	6.0	0.4	6.7	0.7	3.9	15.6	14.5	16.2	9.9	12.2	6.0	5.5	6.5	16.0	0.5	0.5	--	12.6	14.0
6	10.5	12.0	5.9	1.7	--	2.7	0.2	2.0	13.4	7.5	13.4	14.5	23.0*	13.4	13.0	11.5	13.5	1.4	1.5	--	13.5*	18.0*
7	4.9	5.8	2.3	--	--	1.4	0.2	1.2	9.9	5.0	8.8	16.3*	23.0*	17.7*	18.0*	15.5*	13.5	1.7	4.0	1.5	12.4	16.8
8	1.5	2.7	0.5	--	--	1.3	0.1	1.1	6.0	2.5	3.3	14.8	14.8	16.4	16.0	14.0	16.5*	1.4	6.5	3.9	11.5	12.2
9	0.3	1.0	--	--	--	0.9	--	0.4	3.7	0.5	0.9	11.9	11.2	13.8	13.5	9.5	14.0	2.9	8.0	7.4	11.5	8.2
30	--	--	--	--	--	0.3	--	--	2.0	--	0.6	7.0	8.2	10.8	11.5	7.5	7.0	6.2	9.0	11.8	9.3	5.2
1	--	--	--	--	--	--	--	--	0.6	--	0.3	4.1	2.6	5.6	7.5	10.0*	2.5	8.8	7.5	11.8	6.2	2.4
2	--	--	--	--	--	--	--	--	--	--	--	3.2	--	2.2	4.5	10.0*	2.0	11.2	7.0	10.8	3.9	0.9
3	--	--	--	--	--	--	--	--	--	--	--	1.7	--	1.7	3.5	5.0	1.0	13.8	8.0	13.7	1.7	0.3
4	--	--	--	--	--	--	--	--	--	--	--	1.5	--	1.7	1.5	1.0	--	14.0*	8.5	14.7*	0.3	--
5	--	--	--	--	--	--	--	--	--	--	--	1.1	--	1.3	--	--	--	12.1	10.5	11.8	--	--
6	--	--	--	--	--	--	--	--	--	--	--	0.3	--	0.4	--	--	--	8.8	12.5*	7.4	--	--
7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	6.2	10.0	3.4	--	--
8	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	4.8	4.5	1.5	--	--
9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.9	1.5	0.5	--	--
40	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.9	0.5	--	--	--
1	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.2	--	--	--	--
2	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--	0.2	--	--	--	--
Number of fish	81	73	55	58	181	181	203	140	88	50	82	86	49	58	50	50	50	105	50	51	89	82

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1964.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956, ages 1. and 2. combined.
[7] 1963.
[8] 1965.
[9] 1961.
[10] 1967.
* Indicates modes.

TABLE 6.—Percentage frequency distribution[1] of circuli in the total freshwater zone of age 2. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska										British Columbia	
	Ozernaya River[2]	Blizhnee Lake[3]	Dalnee Lake[3]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[9]	Chignik[7]	Cook Inlet[8]	Karluk River[9]	Yakutat[5]	Ketchikan[10]	Nass River[5]	Nimpkish River[11]
	Percent														
9	--	0.5	--	--	--	0.4	--	--	--	--	--	--	--	--	--
10	--	2.9	--	--	--	2.4	--	--	1.2	--	--	--	--	--	--
1	--	10.3	--	--	--	5.5	--	--	8.5	--	--	2.4	--	--	--
2	0.3	18.6	--	--	--	9.3	--	--	16.1*	--	--	6.0	--	--	--
3	0.7	20.1*	--	1.2	--	12.9	--	--	13.3	0.3	--	11.9	--	--	--
4	0.7	16.2	--	4.5	0.2	14.0*	--	--	7.7	3.0	--	20.2*	0.5	--	--
5	2.4	11.3	--	8.2	1.9	12.1	--	0.9	7.3	6.9	--	19.0	4.0	--	--
6	5.6	6.9	--	12.7	4.4	8.8	--	3.7	9.7	10.2	0.5	13.1	8.5	1.1	--
7	9.4	4.4	--	16.4*	6.8	7.9	0.2	6.9	12.5	11.8*	4.0	11.9	11.5	5.7	--
8	14.6	3.9	--	16.4*	10.0	7.4	0.4	7.9	12.1	11.5	10.0	8.3	15.5	10.2	1.0
9	16.3*	2.9	--	13.9	11.9	4.8	0.9	7.9	7.3	10.9	12.5	3.6	16.5*	13.6	3.1
20	14.6	1.5	--	9.4	13.1	3.3	2.5	10.2*	2.4	11.5	12.0	2.4	13.5	19.3*	5.2
1	13.2	0.5	--	7.0	14.8*	2.6	5.8	10.2*	0.4	11.8*	15.0	1.2	11.5	18.2	5.2
2	9.7	--	--	6.6	14.1	2.4	9.7	6.9	--	10.5	18.5*	--	9.5	10.2	3.1
3	5.9	--	--	3.3	11.3	2.6	13.1	6.9	0.4	5.9	14.5	--	5.5	8.0	2.1
4	4.2	--	--	0.4	7.4	1.4	15.5*	9.2	0.8	2.6	7.0	--	1.5	8.0	2.1
5	2.1	--	--	--	3.0	0.7	15.3	9.7	0.4	1.3	3.5	--	--	4.5	2.1
6	0.3	--	--	--	0.8	0.9	13.3	7.9	--	0.3	2.0	--	0.5	1.1	3.1
7	--	--	0.7	--	0.2	0.4	10.2	5.1	--	0.3	0.5	--	1.0	--	5.2
8	--	--	5.3	--	--	--	6.5	2.8	--	0.7	--	--	0.5	--	4.2
9	--	--	10.5	--	--	--	3.2	1.9	--	0.3	--	--	--	--	2.1
30	--	--	11.2	--	--	--	1.3	1.4	--	--	--	--	--	--	3.1
1	--	--	12.5	--	--	--	0.7	0.5	--	--	--	--	--	--	4.2
2	--	--	16.4*	--	--	--	0.5	--	--	--	--	--	--	--	7.3
3	--	--	16.4*	--	--	--	0.4	--	--	--	--	--	--	--	12.5*
4	--	--	10.5	--	--	--	0.4	--	--	--	--	--	--	--	11.5
5	--	--	5.9	--	--	--	0.2	--	--	--	--	--	--	--	6.2
6	--	--	5.3	--	--	--	--	--	--	--	--	--	--	--	4.2
7	--	--	3.9	--	--	--	--	--	--	--	--	--	--	--	5.2
8	--	--	1.3	--	--	--	--	--	--	--	--	--	--	--	5.2
9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.1
Number of fish	72	51	38	61	216	105	139	54	62	76	50	21	50	22	24

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1959.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956.
[7] 1961.
[8] 1963.
[9] 1965.
[10] 1964.
[11] 1967.
* Indicates modes.

DESCRIPTION OF SCALES FROM FISH OF VARIOUS AREAS

The scale photographs are shown in three major series: ages 1., 2., and 3. Representative scales from each broad coastal area with relatively similar scales (including specific scale types from some areas of small production, when necessary) are shown on one plate. Two exceptions to this grouping are made: (1) distinctive scales from age 1. fish from North American areas are shown on two plates and those for age 2. fish on one plate; and (2) scales from fish from North American areas north of Bristol Bay of ages 1., 2., and 3. are shown on the same plate. Scales of age 0. fish from all areas are shown on one plate, and those of age 4. fish from all areas are shown on another plate.

A reference to the appropriate frequency tables of the number of circuli in the freshwater and first ocean zones (Tables 4 to 8) is made for each area group. These tables should be referred to as scales from each group are discussed.

TABLE 7.—Percentage frequency distribution[1] of circuli in the first ocean zone of age 2. sockeye salmon collected in various years from 1956 to 1967.

Number of circuli	Asia			Alaska										British Columbia	
	Ozernaya River[2]	Blizhnee Lake[3]	Dolnee Lake[4]	Far North[4]	Bristol Bay[5]	Attu Island[6]	Adak Island[6]	Unalaska Island[6]	Chignik[7]	Cook Inlet[8]	Karluk River[9]	Yakutat[5]	Ketchikan[10]	Nass River[5]	Nimpkish River[11]
								Percent							
11	--	--	--	--	--	--	0.9	--	--	--	--	--	--	--	--
2	--	--	--	--	--	--	2.7	--	--	--	--	--	--	--	--
3	--	--	--	--	--	0.1	5.9	0.2	--	--	--	--	--	--	--
4	--	--	--	--	0.3	0.4	10.0	1.2	--	--	--	--	--	--	--
5	--	--	--	--	1.2	0.8	12.6	3.4	--	--	--	--	--	--	--
6	--	--	--	--	3.4	1.2	13.3*	5.4	--	--	--	--	--	--	--
7	--	--	2.0	2.0	8.0	2.6	13.2	7.0	--	--	--	--	--	--	--
8	--	--	5.3	7.0	13.1	5.1	10.8	9.6	--	--	--	--	--	--	--
9	0.3	--	7.9	9.8	17.9	7.3	8.4	13.7	--	0.7	0.5	--	--	--	--
20	1.7	1.0	13.8	12.7	20.9*	12.6	7.4	14.8*	0.4	3.0	1.5	--	--	--	--
1	3.1	5.9	21.1*	16.4*	17.8	16.9*	5.8	11.2	4.0	6.9	4.5	--	0.5	--	--
2	6.6	11.8	21.1*	15.6	10.5	14.9	3.8	9.5	8.1	9.5	7.5	--	2.0	--	--
3	16.0	13.2	13.8	13.5	4.5	13.2	2.3	8.9	8.9	10.9	8.5	2.4	3.5	--	--
4	24.0*	14.7	7.9	10.7	1.5	11.5	1.5	6.4	11.3	15.5	12.5	14.3	5.0	1.1	1.0
5	22.2	18.6*	5.3	6.6	0.5	6.7	0.7	3.9	14.5	18.4*	15.0	25.0*	10.0	3.4	3.1
6	14.2	16.7	2.0	3.7	0.2	2.7	0.2	2.0	16.1	13.8	14.5	21.4	15.0*	8.0	5.2
7	7.3	9.3	--	1.6	0.1	1.4	0.2	1.2	16.9*	9.2	16.5*	16.7	14.5	20.5	6.2
8	3.5	4.9	--	0.4	--	1.3	0.1	1.1	13.3	6.9	13.5	13.1	13.0	29.5*	8.3
9	1.0	2.5	--	--	--	0.9	--	0.4	5.6	3.3	5.0	6.0	12.5	21.6	16.7
30	--	1.0	--	--	--	0.3	--	--	0.8	1.3	0.5	1.2	10.0	9.1	22.9*
1	--	0.5	--	--	--	--	--	--	--	0.7	--	--	6.5	2.3	16.7
2	--	--	--	--	--	--	--	--	--	--	--	--	4.5	--	8.3
3	--	--	--	--	--	--	--	--	--	--	--	--	2.5	1.1	5.2
4	--	--	--	--	--	--	--	--	--	--	--	--	0.5	2.3	2.1
5	--	--	--	--	--	--	--	--	--	--	--	--	--	1.1	1.0
6	--	--	--	--	--	--	--	--	--	--	--	--	--	--	2.1
7	--	--	--	--	--	--	--	--	--	--	--	--	--	--	1.0
Number of fish	72	51	38	61	216	191	203	140	62	76	50	21	50	22	24

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1959.
[3] 1958.
[4] 1957.
[5] 1966.
[6] 1956, ages 1 and 2 combined.
[7] 1961.
[8] 1963.
[9] 1956.
[10] 1964.
[11] 1967.
* Indicates modes.

KEY TO THE PLATES

To compensate for the reduction of the original scale photographs to fit the printed page, use a 3 to 5× reading or magnifying glass to study them.

The area enclosed by the first or central circulus is the focus or central platelet of the scale.

The long black pointers near the focus indicate winter marks in the freshwater growth zone.

A black stub pointer, if present, indicates the end of plus or transitional growth. If plus growth is present, the circuli between the outermost long black pointer and the black stub pointer are plus growth circuli. If no plus growth is present, the outermost black pointer indicates the end of freshwater growth as well as the last winter in fresh water.

The white pointers bordered by black indicate the first winter mark in the ocean growth. The circuli between the end of the freshwater growth (or plus growth, if present) and this pointer are ocean-growth circuli and record the first year's growth in the ocean (the first ocean growth zone). The more widely spread circuli of this zone were deposited from May or June to September or October (the summer growth), whereas the more closely spaced circuli near the pointer were deposited during the autumn, winter, and early spring months (the winter growth).

If a small white pointer is present, it indicates an adventitious check in the first ocean growth

TABLE 8.—Percentage frequency distribution[1] of circuli (A) in the total freshwater zone and (B) in the first ocean zone of age 3. sockeye salmon collected in various years from 1955 to 1964.

Number of circuli	(A) Asia			(A) North America		(B) Asia			(B) North America	
	Asia[2]	Blizhnee Lake[3]	Dalnee Lake[4]	Bristol Bay[5]	Karluk River[6]	Asia[2]	Blizhnee Lake[3]	Dalnee Lake[4]	Bristol Bay[5]	Karluk River[6]
	Percent									
12	--	0.6	--	--	--	--	--	--	--	--
3	--	4.1	--	--	--	--	--	--	--	--
4	--	9.9	--	--	--	--	--	--	0.4	--
5	0.5	15.1	--	--	--	--	--	--	1.2	--
6	2.9	19.2*	--	--	--	--	--	--	3.3	--
7	8.8	17.4	--	--	--	--	--	--	7.1	--
8	15.9	11.6	--	--	--	--	--	2.7	12.1	--
9	18.1*	9.9	--	1.0	--	1.0	--	8.1	17.9	0.3
20	16.9	8.1	--	2.0	--	2.9	--	10.1	19.6*	1.9
1	14.5	3.5	--	4.0	1.0	5.9	--	11.5	15.4	4.8
2	7.8	0.6	--	10.0	3.2	10.8	1.2	16.9	10.8	7.6
3	2.2	--	--	12.0	6.6	16.4	5.8	18.9*	6.7	13.0
4	1.2	--	--	13.0	9.5	20.1*	12.2	15.5	2.9	20.2
5	1.5	--	--	19.0*	11.4	19.1	15.1	10.8	1.7	20.9*
6	1.2	--	--	17.0	13.3	13.5	16.3	4.7	0.8	14.8
7	1.7	--	--	10.0	12.7	6.4	18.0*	0.7	--	8.6
8	2.5	--	0.7	6.0	12.1	2.2	16.3	--	--	3.8
9	2.0	--	4.1	3.0	14.2*	1.2	10.5	--	--	1.9
30	1.2	--	8.1	2.0	10.2	0.5	4.1	--	--	1.6
1	0.7	--	8.1	1.0	4.1	--	0.6	--	--	0.6
2	0.2	--	6.1	--	1.2	--	--	--	--	--
3	--	--	8.1	--	0.3	--	--	--	--	--
4	--	--	11.5*	--	--	--	--	--	--	--
5	--	--	8.1	--	--	--	--	--	--	--
6	--	--	6.8	--	--	--	--	--	--	--
7	--	--	11.5*	--	--	--	--	--	--	--
8	--	--	11.5*	--	--	--	--	--	--	--
9	--	--	8.1	--	--	--	--	--	--	--
40	--	--	4.1	--	--	--	--	--	--	--
1	--	--	0.7	--	--	--	--	--	--	--
2	--	--	--	--	--	--	--	--	--	--
3	--	--	--	--	--	--	--	--	--	--
4	--	--	--	--	--	--	--	--	--	--
5	--	--	--	--	--	--	--	--	--	--
6	--	--	0.7	--	--	--	--	--	--	--
7	--	--	1.4	--	--	--	--	--	--	--
8	--	--	0.7	--	--	--	--	--	--	--
Number of fish	102	43	37	25	79	102	43	37	25	79

[1] Actual frequencies smoothed according to Henry (1961).
[2] 1962, from an area off southeast Kamchatka.
[3] 1958.
[4] 1964.
[5] 1955 and 1957 combined.
[6] 1961.
* Indicates modes.

zone. Adventitious checks in other zones are not noted.

AGE 0., ALL AREAS (Plate 1)

As noted previously, age 0. sockeye salmon are not common anywhere since fish of this species normally live for one or more years in a lake before migrating to the sea. Consequently, it was not possible to assemble frequency distributions of the number of circuli in the first ocean zone for age 0. fish. It appears, however, that usually there are a few more circuli in the first ocean zone of scales of age 0. than on scales from fish of the same geographical area that have lived one or more years in fresh water.

A few individuals of this age have been found at some time in almost every locality. Gilbert

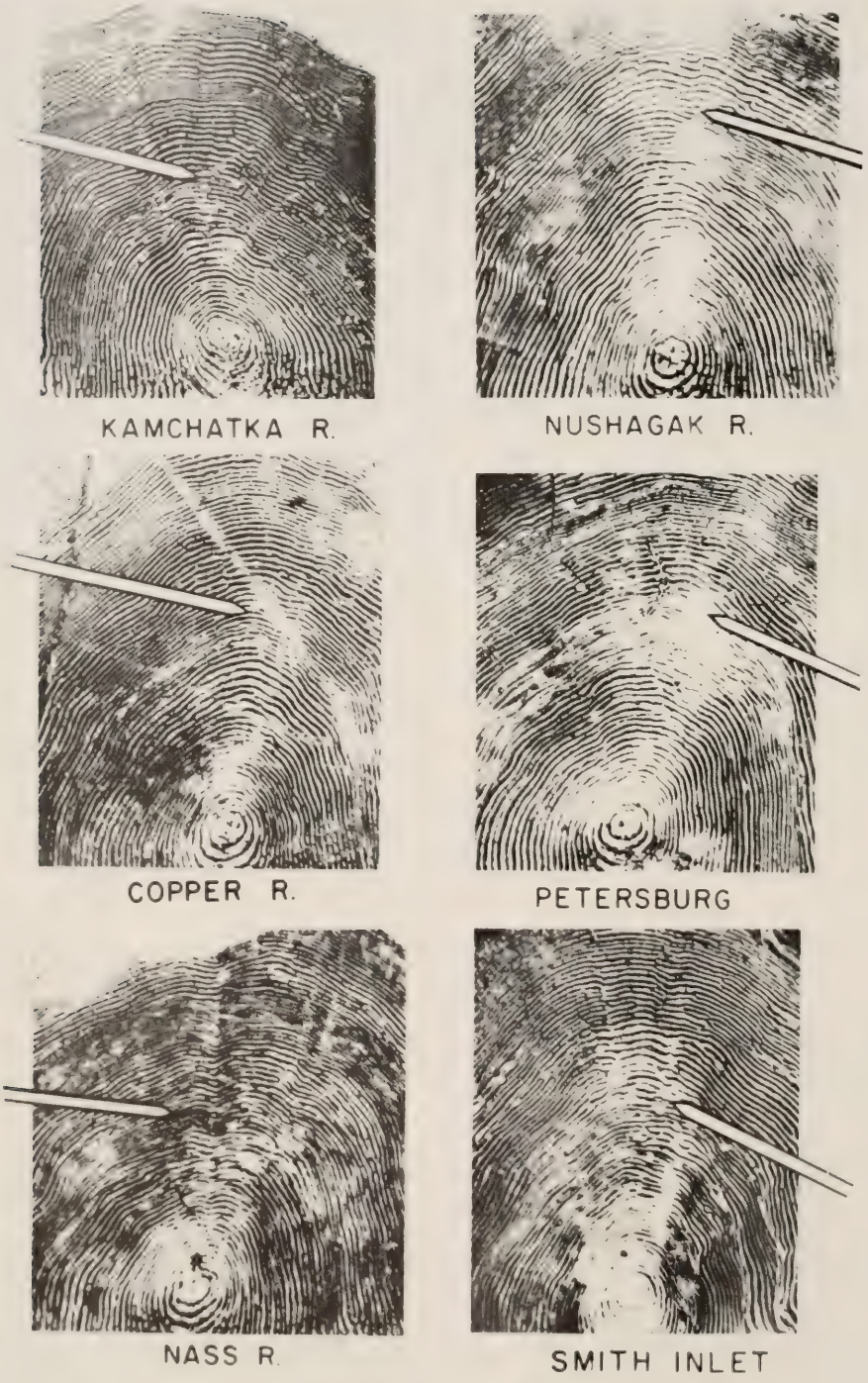


PLATE 1.—Age 0., all areas.

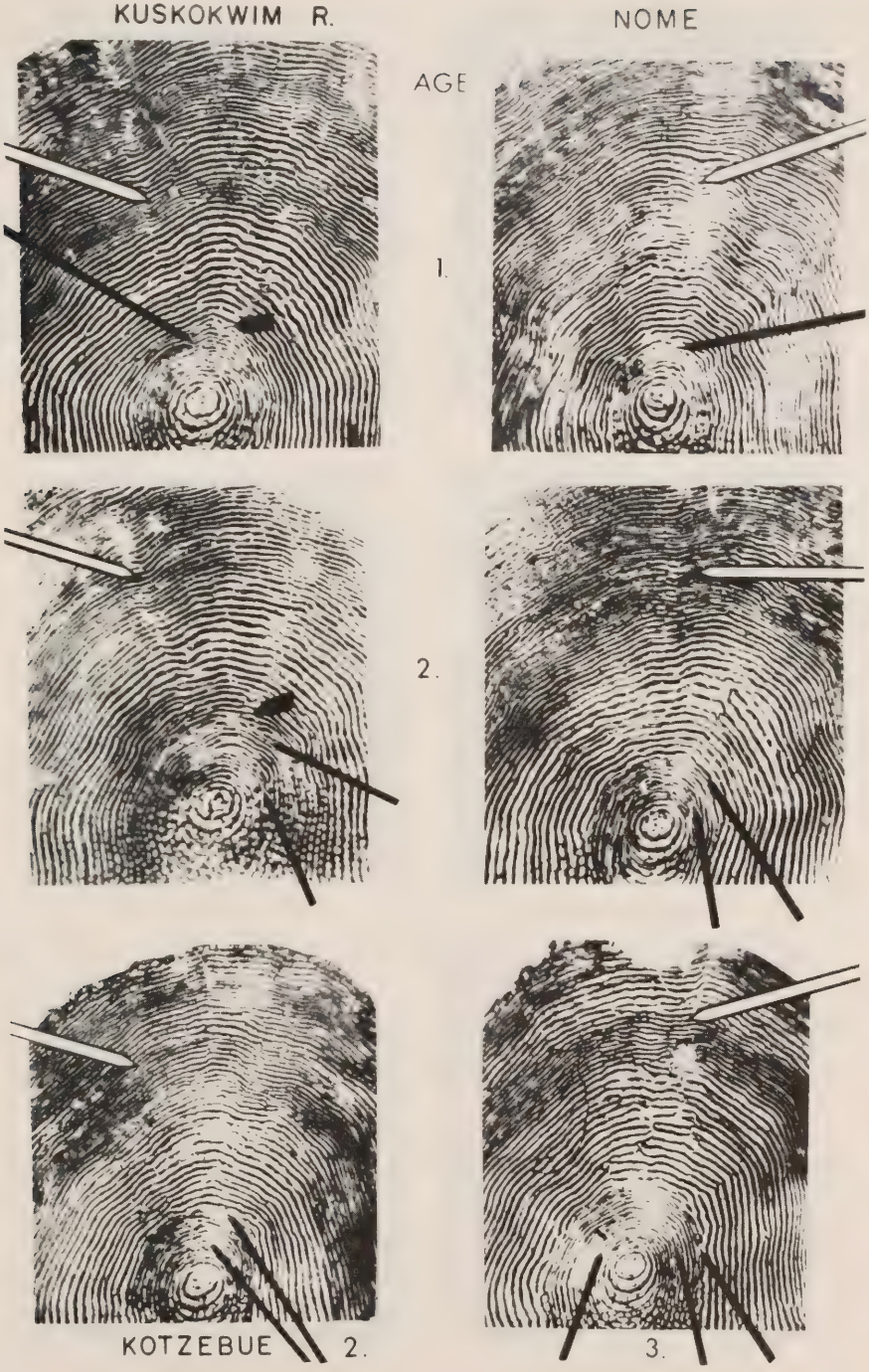
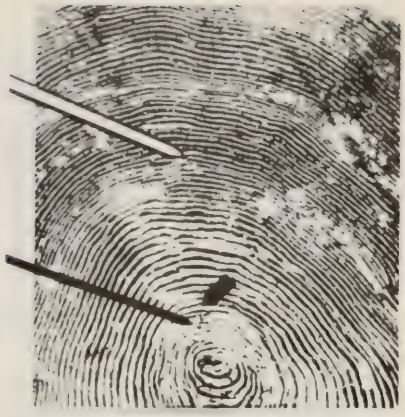
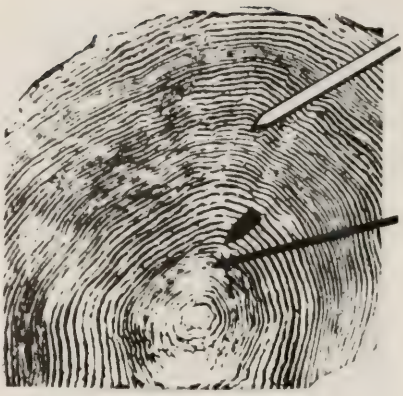


PLATE 2.—Ages 1., 2., and 3., Alaskan areas north of Bristol Bay.

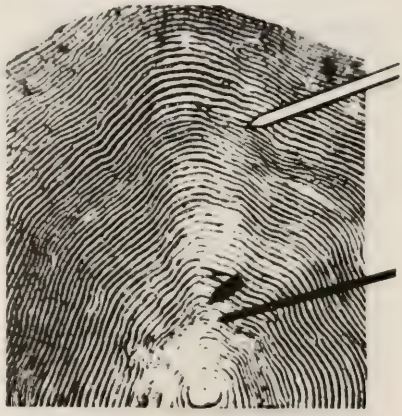


KAMCHATKA R.



OZERNAYA R.

BOLSHAYA R.



OKHOTSK SEA

LAKE BLIZHNEE

LAKE DALNEE

PLATE 3.—Age 1., Asia.

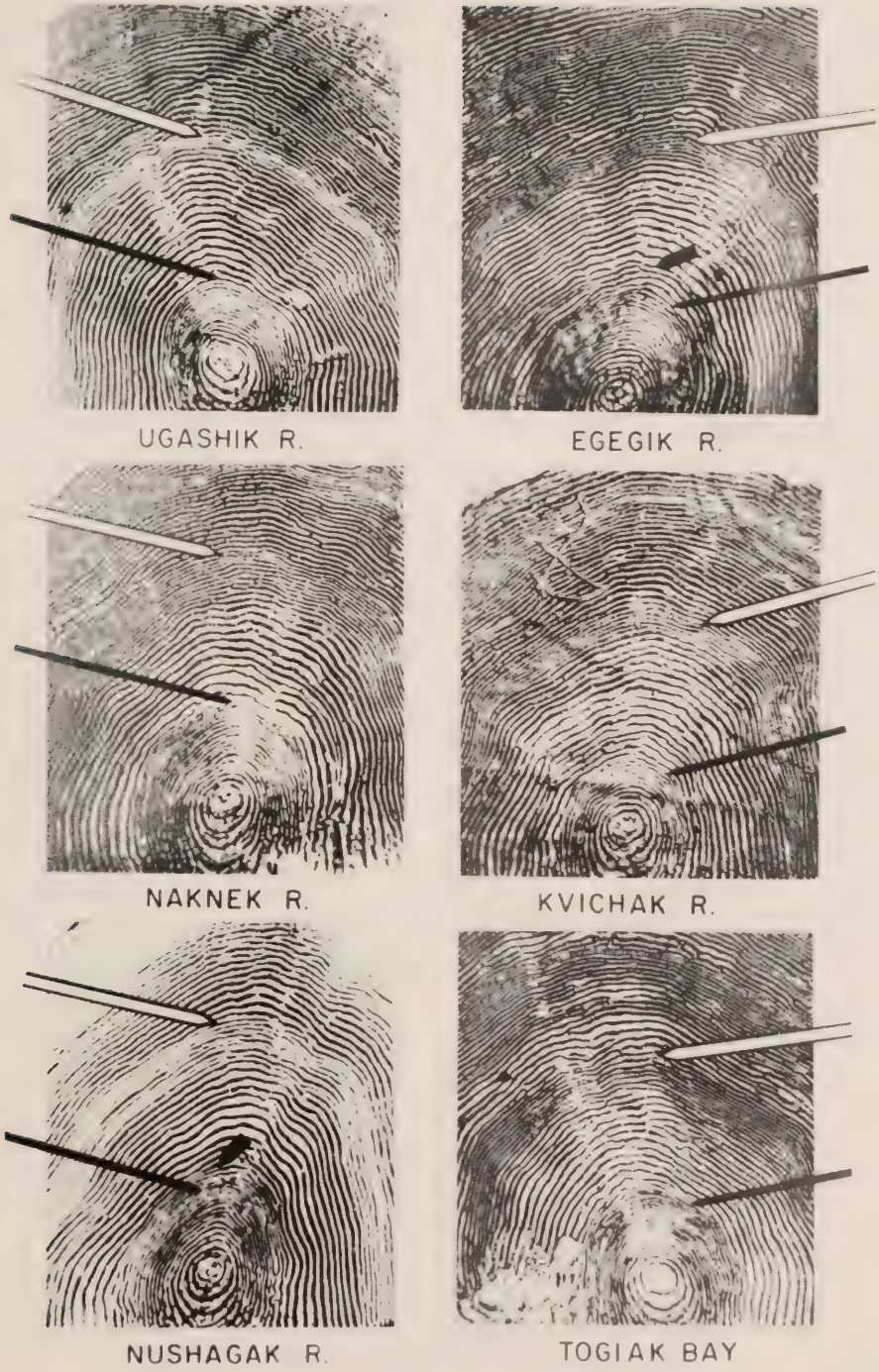


PLATE 4.—Age 1., Bristol Bay.

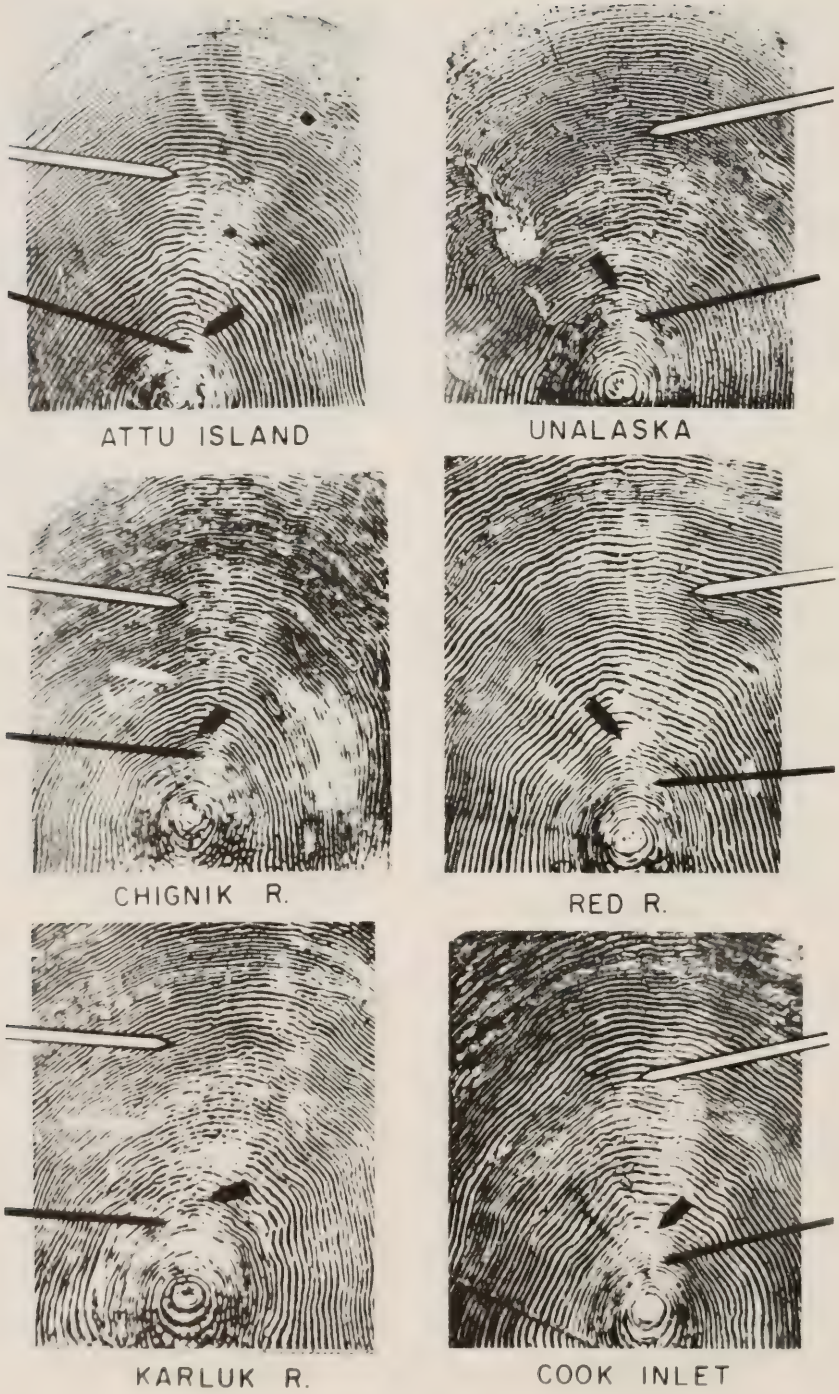


PLATE 5.—Age 1., Aleutian Islands to Cook Inlet.

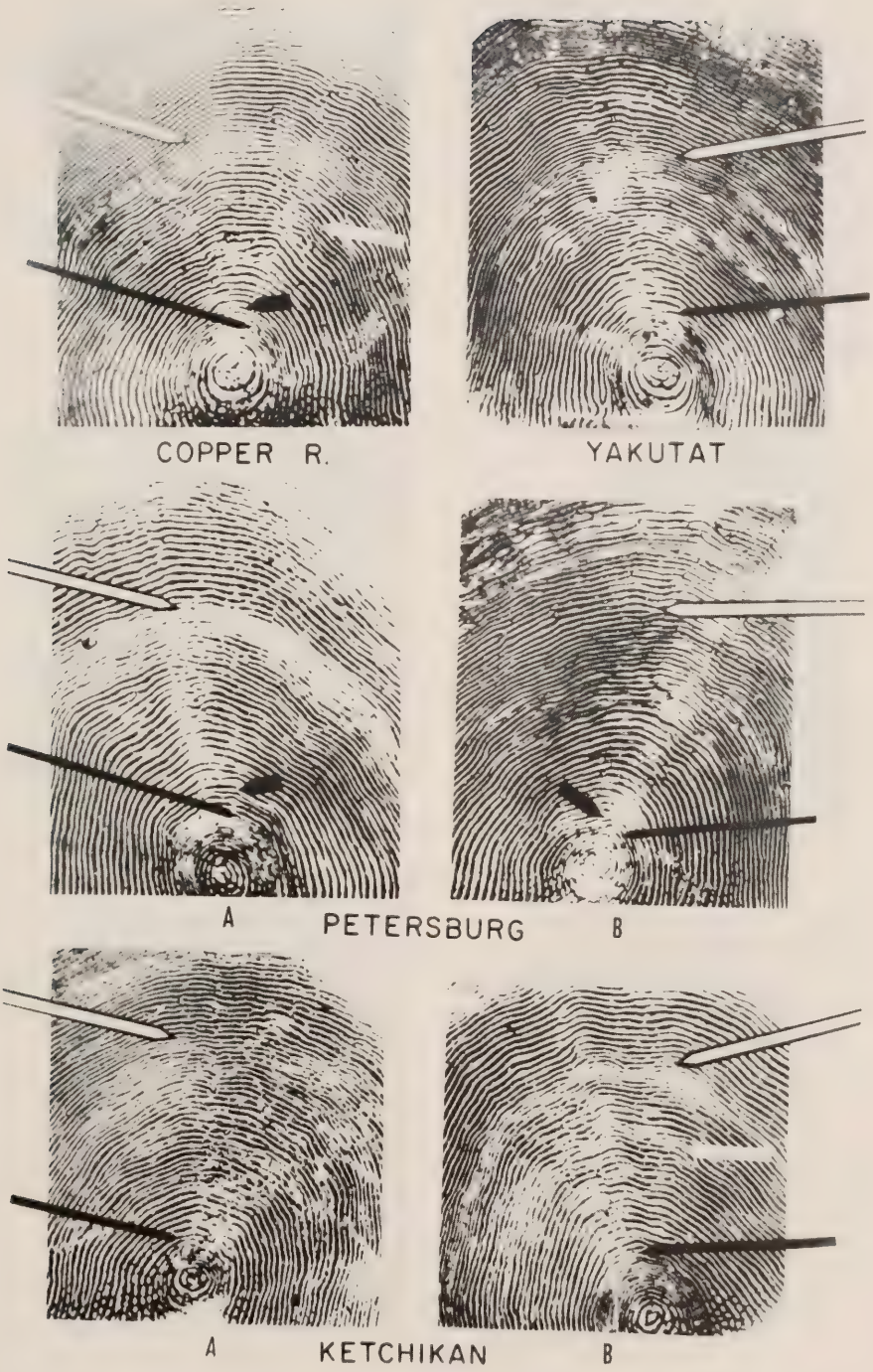


PLATE 6.—Age 1., Copper River to southeastern Alaska.

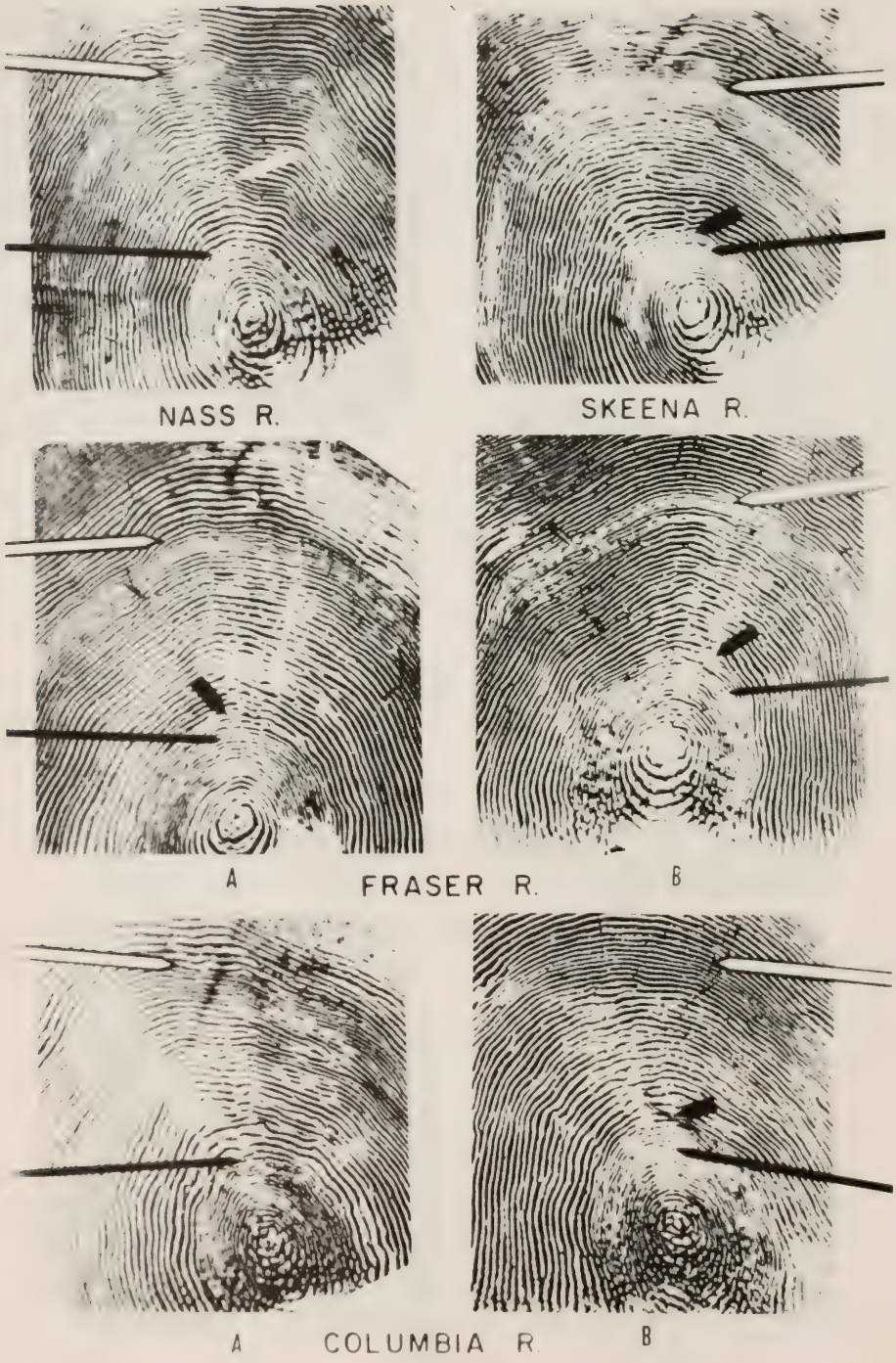


PLATE 7.—Age 1., British Columbia and the Columbia River.

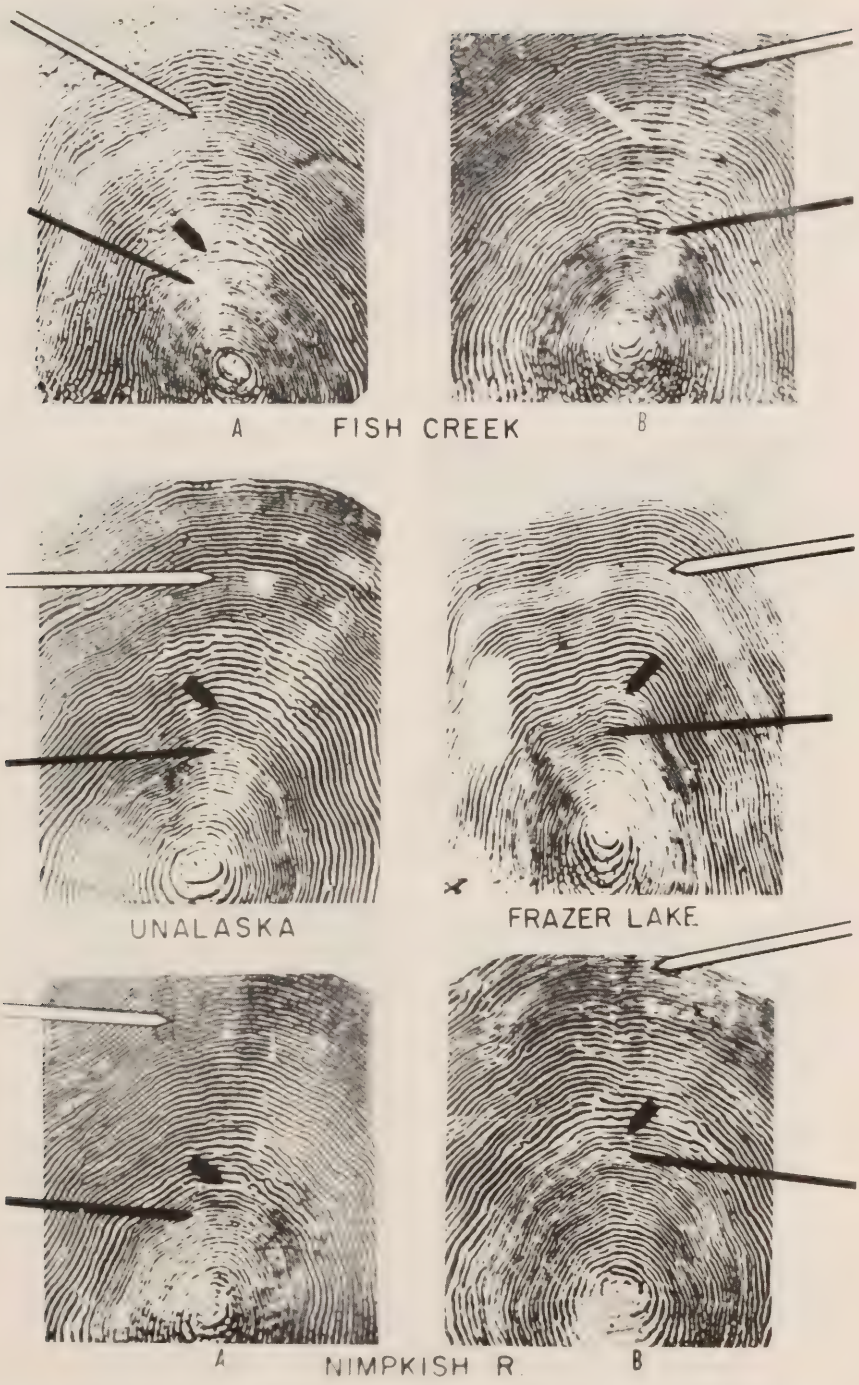


PLATE 8.—Age 1., North American areas with distinctive scales, Fish Creek type.

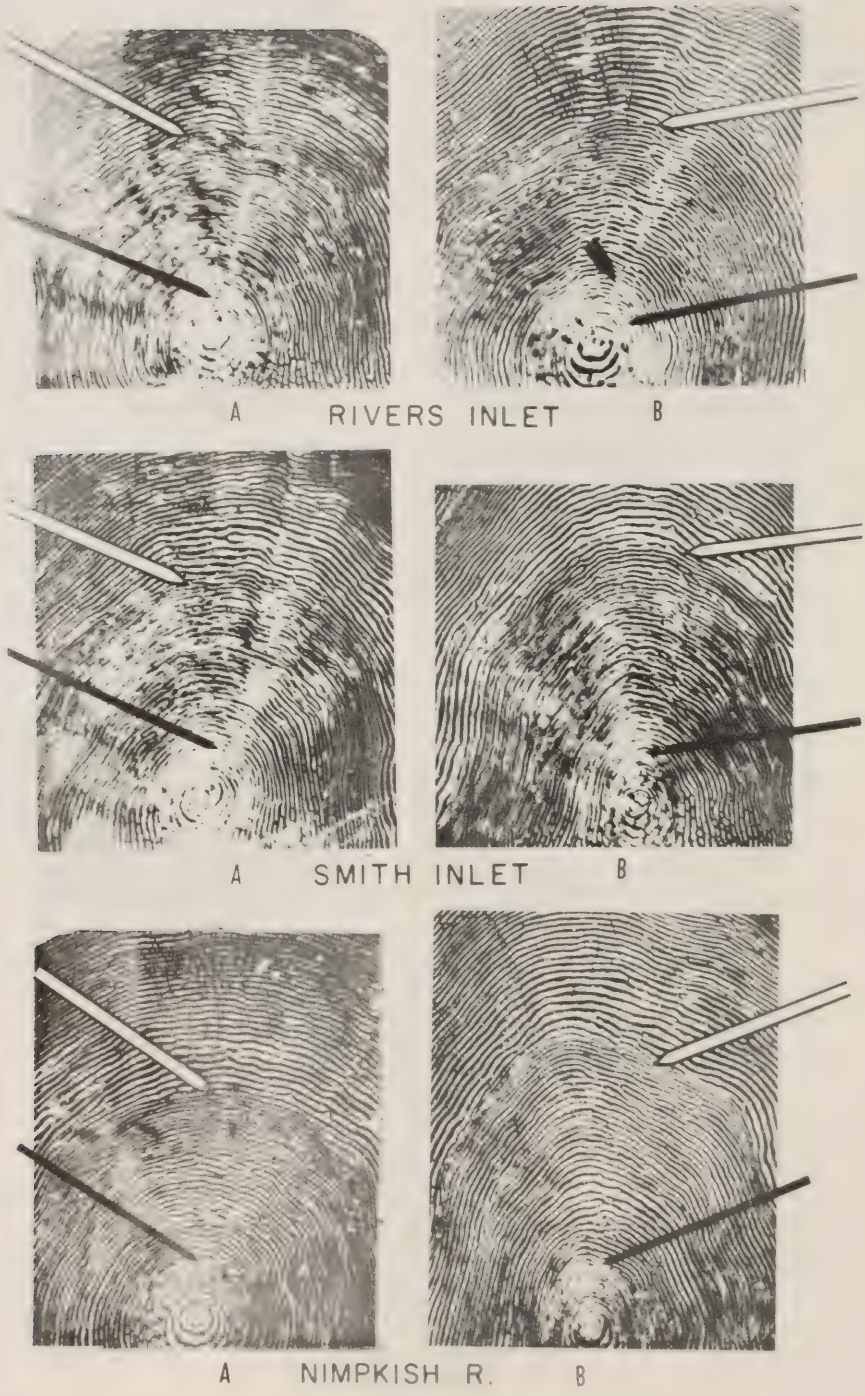


PLATE 9.—Age 1., North American areas with distinctive scales, Rivers Inlet type.

PLATE 10.—Age 2., Asia.

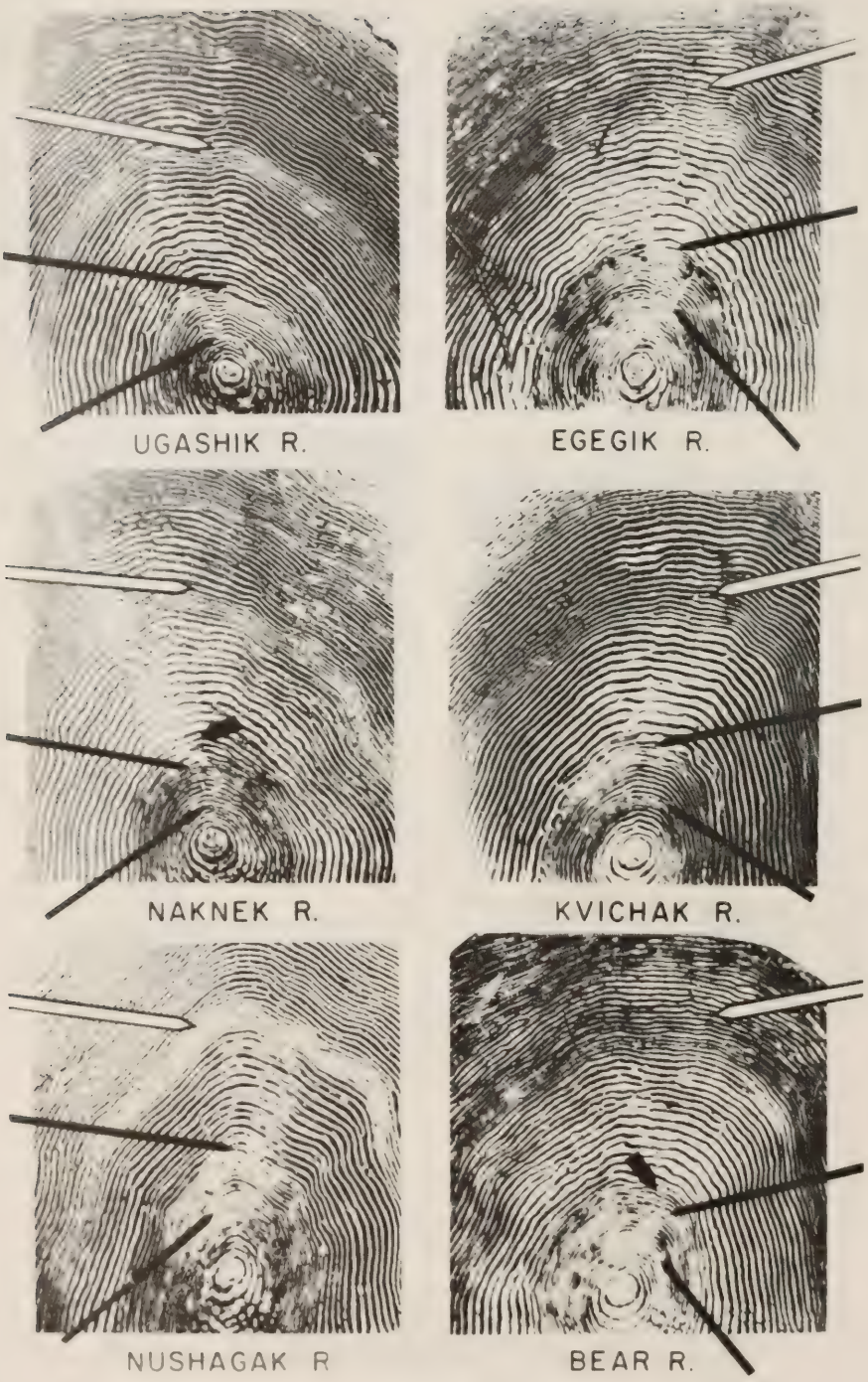


PLATE 11.—Age 2., Bristol Bay.

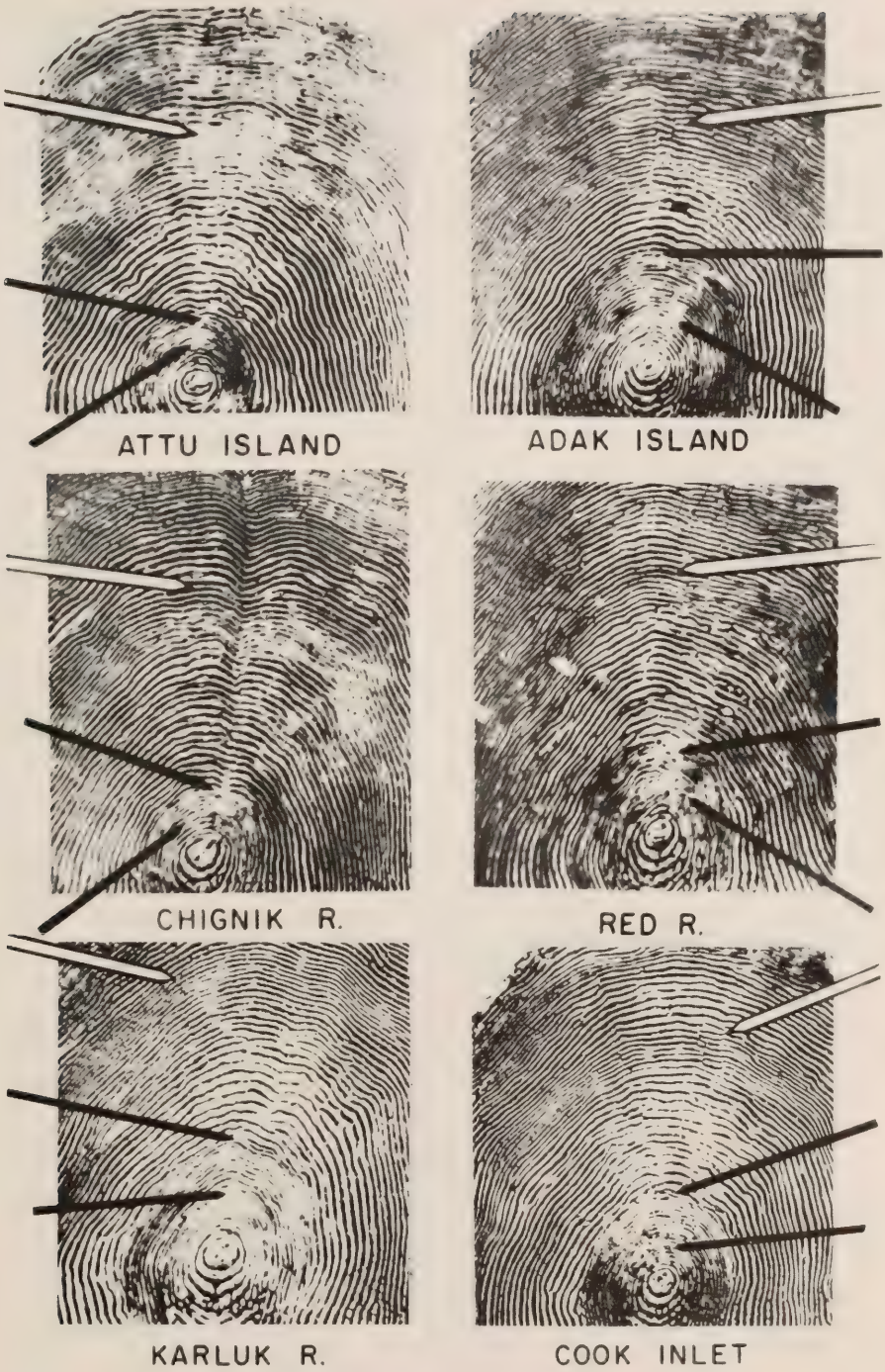


PLATE 12.—Age 2., Aleutian Islands to Cook Inlet.

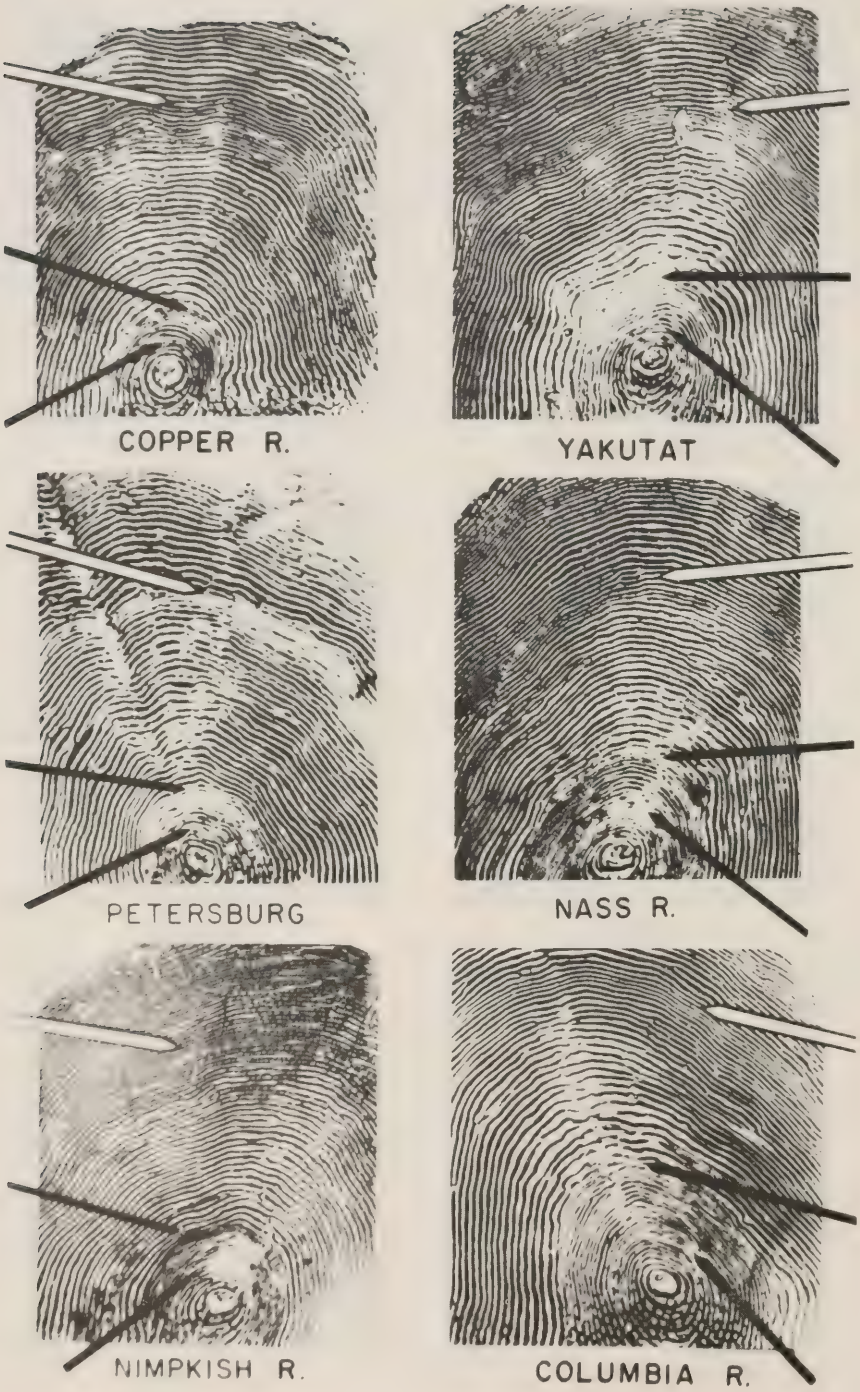


PLATE 13.—Age 2., Copper River to the Columbia River.

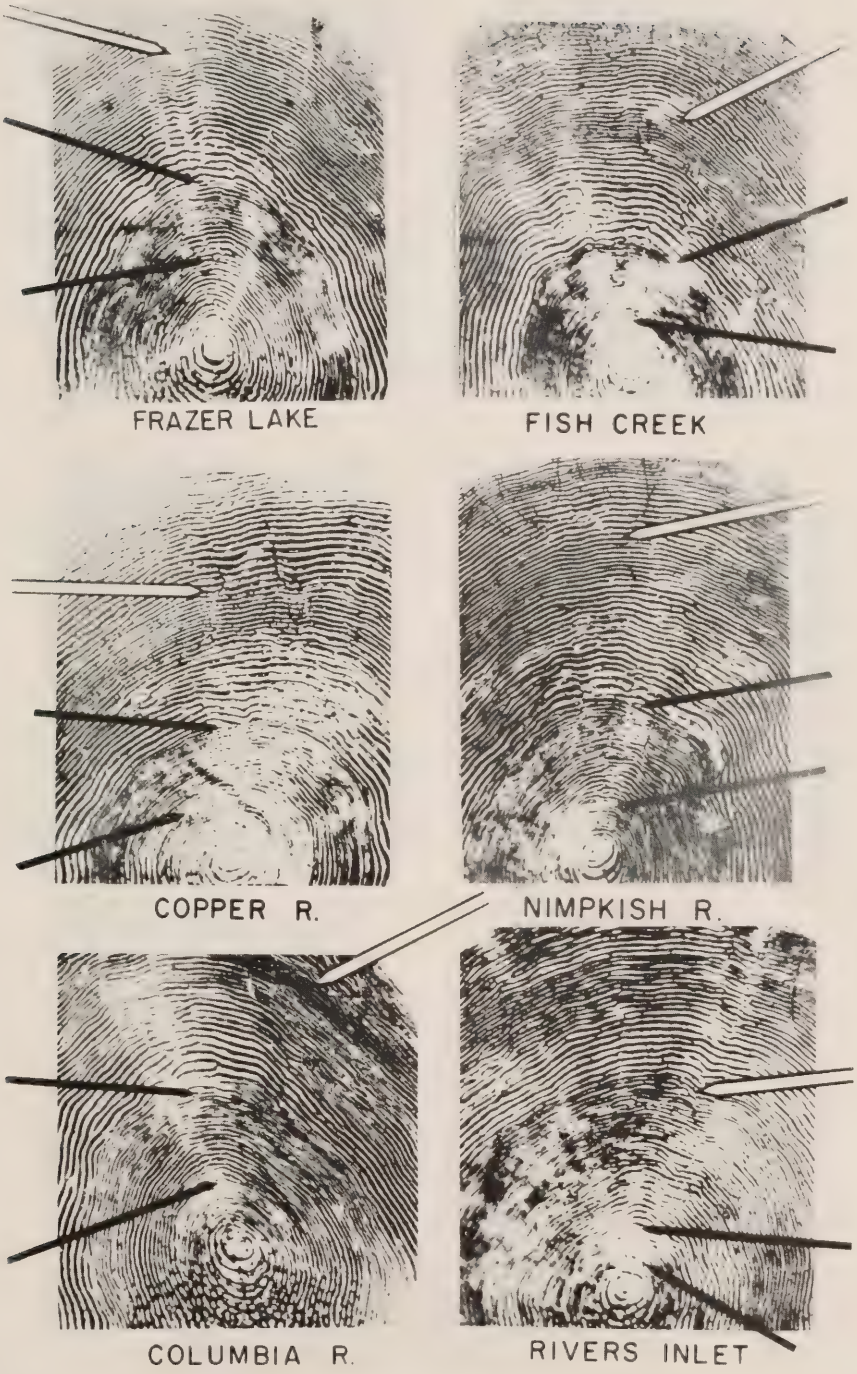


PLATE 14.—Age 2., North American areas with some distinctive scales.

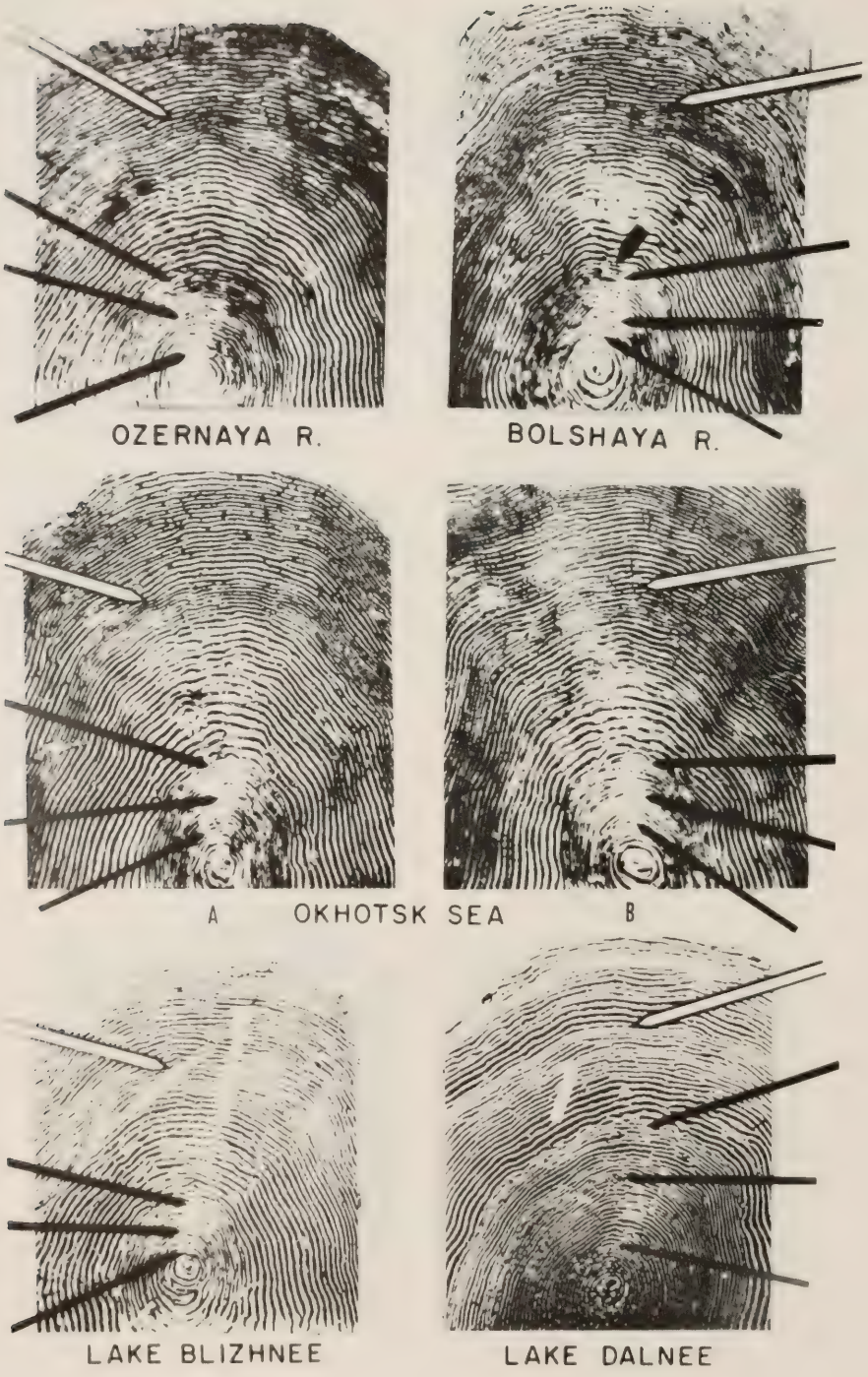


PLATE 15.—Age 3., Asia.

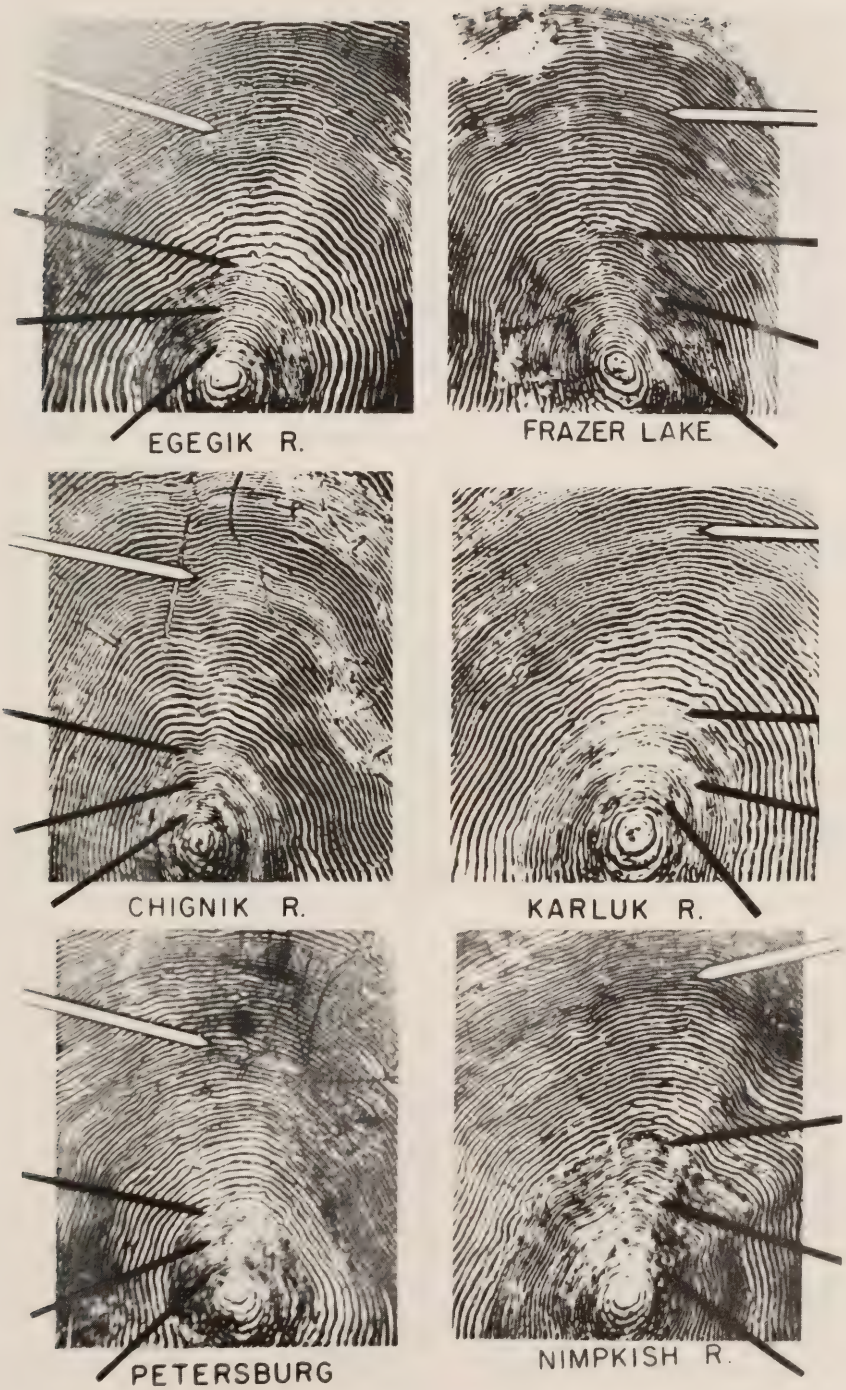


PLATE 16.—Age 3., North America, all areas.

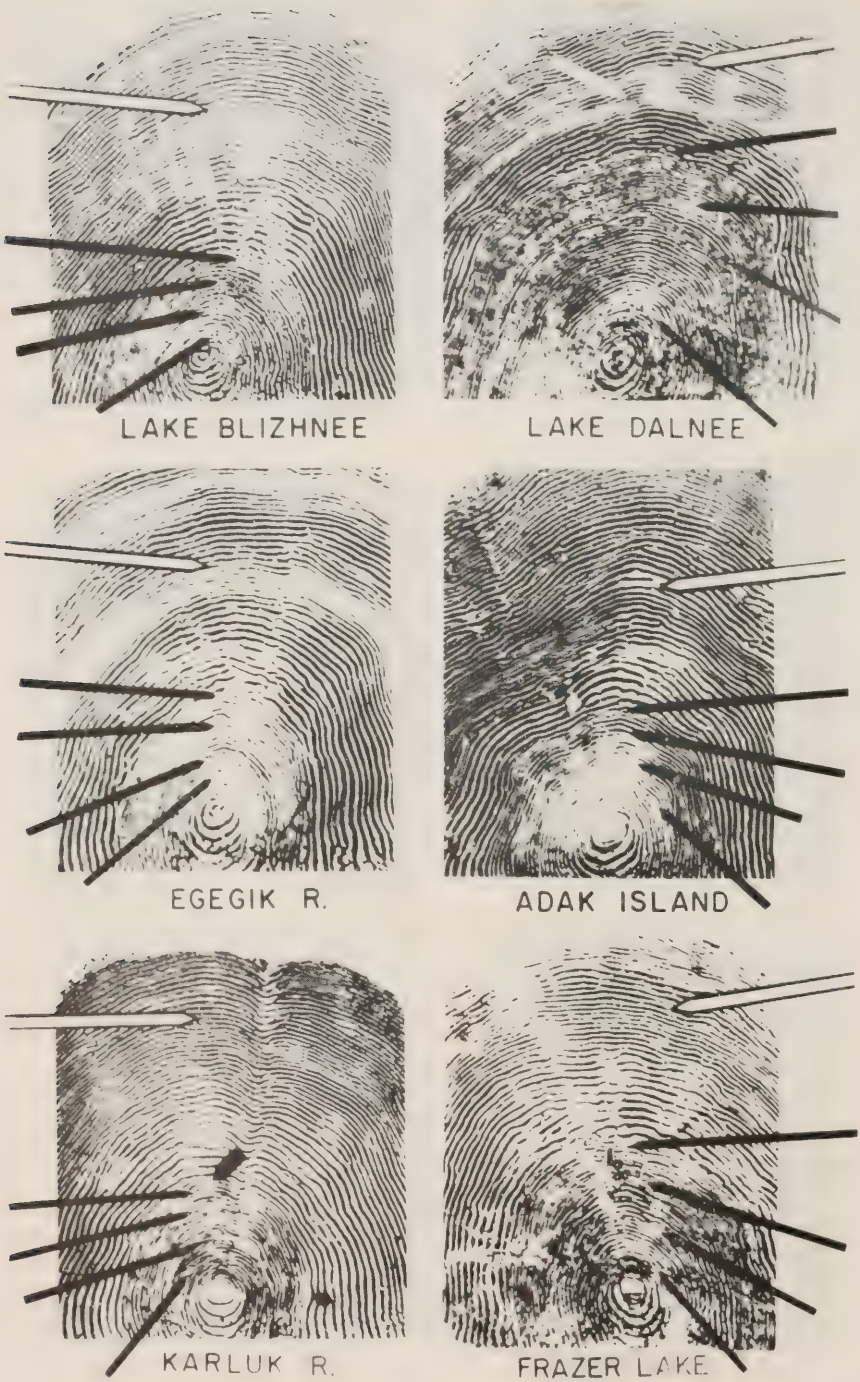


PLATE 17.—Age 4., all areas.

(1919) reported a stock spawning in the Harrison River, B.C., near its junction with the Fraser, B.C., and Krogius (1958) noted that they occurred in the Kamchatka, Bolshaya, and Paratunka Rivers, USSR. The Nushagak River, Bristol Bay, Alaska, had more than the usual number of individuals of this age in 1961 (Koo, 1962b) but not enough fish from which to take scales to furnish a frequency distribution.

Except for the Rivers Inlet, B.C., fish, there is little difference between areas in the features of the scales of this freshwater age. Scales from individuals taken from the Copper River, Alaska, southward to the Fraser River, however, tend to have a few more circuli in the first ocean zone than those from Bristol Bay, Alaska.

Fish of this age from Rivers Inlet and Smith Inlet, B.C., can be identified to that geographical area because the first ocean zone has the fine-textured circuli typical of most fish from these areas regardless of the freshwater age of the fish (see Plates 9 and 14).

AGE 1., 2., and 3., ALASKAN AREAS NORTH OF BRISTOL BAY (Plate 2; Tables 4, 5, 6, and 7)

Production of sockeye salmon north of Bristol Bay is small. The Kuskokwim River is the largest producer in the area. In the Norton Sound (Nome) and Kotzebue areas, few sockeye salmon are found. However, they are heavily exploited when present along with the other species—by local residents for food and barter—and thus are important in the local economy, especially in some years.

Very little is known of the migrations and ocean distribution of sockeye salmon originating in areas north of Bristol Bay. Of the many thousands of sockeye tagged by Japanese and United States scientists near the central Aleutian Islands, only two tagged near Attu Island in 1958 and one tagged near Kiska Island in 1960 have been returned from the area north of Bristol Bay. All three were recaptured in the Kuskokwim River (Hartt, 1966).

Presently it is not possible to identify the origin of most of the sockeye salmon from this area that are caught in offshore waters because the scales resemble those from many fish from Asia and Alaska Peninsula.

All freshwater age groups of sockeye salmon from north of Bristol Bay have small freshwater zones with few, often broken and irregular circuli in each zone. Some scales show plus growth (see Mosher, 1968, p. 251-254).

Circuli of the first ocean zone are widely and evenly spaced as in scales from Asian fish or those from the Alaska Peninsula. The widest spacing of circuli is usually some distance from the freshwater zone. The number of circuli varies from few, like fish from Bristol Bay, to somewhat more, like fish from Asia or Alaska Peninsula areas.

AGE 1., ASIA (Plate 3; Tables 4 and 5)

Scales from fish from the Kamchatka, Ozernaya, and Bolshaya Rivers do not differ much between rivers. The freshwater zone is relatively small with few, often broken and irregular circuli. Often adventitious checks (false winter marks, see p. 275, Mosher, 1968) occur in the freshwater zone of these scales. Scales that I have examined from fish captured in the Okhotsk Sea (which, according to Hanamura, 1966, may be a mixture of runs from the Ozernaya and Bolshaya Rivers and, at times, small numbers of fish from the Okhota and the Kukhtuy Rivers on the northern coast of the Okhtosk Sea and from other small producing streams of southeastern Kamchatka and the Kurile Islands) do not differ much from those of the Ozernaya and Bolshaya Rivers. Krogius (1958) reported that the scales of fish from the Kukhtuy River are similar to those of the Ozernaya River. Very few fish of this freshwater age are found in the Ozernaya River.

Scales from fish from the Paratunka River show two distinct types of freshwater growth; those from Lake Blizhnee have a very small freshwater zone with only a few, mostly broken, irregular circuli; those from Lake Dalnee have a moderately large to large freshwater zone with numerous regular, unbroken circuli. Krogius (1958) reported the favorable conditions for growth of the fish in Lake Dalnee and the much poorer conditions in Lake Blizhnee.

TABLE 9.—Freshwater scale characters of Asian stocks of sockeye salmon (from Krogius, 1958).

Item	Area and number of years in fresh water										
	1 year				2 years				3 years		
	Kamchatka River	Bolshaya River	Dalnee Lake	Blizhnee Lake	Kamchatka River	Ozernaya River	Dalnee Lake	Blizhnee Lake	Kamchatka River	Ozernaya River	Dalnee Lake
Type of circuli	Regular	Irregular	Regular	Irregular	Regular	Irregular	Regular	Irregular	Regular	Irregular	Regular
Years fresh water	*Number of circuli*										
1	10-16	5-10	12-23	9-15	5-10	5-8	6-23	9-13	5-8	5-8	5-15
2	--	--	--	--	10-24	9-13	10-24	5-9	5-8	5-8	5-15
3	--	--	--	--	--	--	--	--	5-8	5-8	5-15

The circuli of the first ocean zone of the scales from the Asian fish are average (some broken, some regular, see p. 255, Mosher, 1968) and more or less uniformly spaced. If there are a few more widely spaced circuli in the zone, they are usually some distance from the freshwater growth.

As can be seen from Table 3, my samples of scales from the Asian areas are quite small. Krogius (1958) reported on some of the scale characteristics of the Asian spawning stocks. Table 9 summarizes the pertinent material from her paper. My scale data generally agree with those she reported.

AGE 1., NORTH AMERICA

Bristol Bay (Plate 4; Tables 4 and 5)

The number and proportion of fish of this freshwater age group varies from year to year in the Bristol Bay rivers, but age 1. fish predominate each year in the Nushagak area as either the 1.2 or 1.3 age groups (Burgner, 1964).[6] Thus this is an important freshwater age group every year in Bristol Bay.

The bulk of the Bristol Bay sockeye salmon are produced in the Ugashik, Egegik, Naknek, Kvichak (including the Branch River), and Nushagak-Wood River systems. The relative importance of each river varies somewhat from year to year, but the Naknek-Kvichak area produces the largest number of fish, especially in the "big" years (see 1965 catch statistics in Appendix Table 1). In addition to these five river systems, there are a few other areas that provide some fish to Bristol Bay. Streams emptying into Togiak Bay and the Bear and Sandy Rivers on the north side of the Alaska Peninsula produce substantial numbers of sockeye salmon in some years. The Togiak area fish are usually of age 1., whereas those of the Bear River are of age 2. generally. The catches of the various areas of Bristol Bay for 1966, as an example, were as follows (International North Pacific Fisheries Commission, 1966):

Area	*Thousands of fish*
Naknek-Kvichak	5,397.6
Egegik	2,101.2
Nushagak-Wood River	1,170.3
Ugashik	445.4
Togiak	119.8
Bear and Sandy Rivers	151.3

Scales from fish of this age from Bristol Bay are quite similar between streams with only minor variations from year to year. Most scales have distinct freshwater and ocean zones with well-marked circuli. The freshwater growth is moderately large with well-spaced, regular, mostly unbroken circuli. Plus growth is sometimes present, especially in the Togiak, Nushagak, Kvichak, and Ugashik Rivers. In most cases it is easily identified on the scales.

The first ocean zone has relatively few circuli. The summer growth circuli are broad and widely spaced, predominantly regular, and unbroken. An area of widely spaced circuli is usually present near the freshwater zone. The ocean zones of scales of Bristol Bay fish have a more "open" appearance than those of fish from any other geographical area. This is the result of (1) a distinct winter zone of a number of closely spaced circuli, sometimes so close that the zone appears like a broad line around the scale (see winter

[6] Burgner, R. L. 1964. Age composition of Nushagak red salmon runs, 1946-63. Univ. Wash., Fish. Res. Inst. Circ. 219, 62 p. (Processed.)

marks labelled "1" on p. 260 of Mosher, 1968); (2) a relatively small number of circuli in the ocean zones; and (3) a wider spacing of the circuli usually near the freshwater zone.

In the other geographical areas, except Adak Island, there are more circuli, on the average, in the first ocean zone on the scales, and the winter zone may be diffuse (see winter marks labelled "3" on p. 260 of Mosher, 1968). These features result in a more even spacing of ocean circuli and a smaller average width per circulus producing a less "open" appearance. The effect of this characteristic is reflected in the size of the widest five adjacent circuli in the first ocean zone in the frequency tabulations shown in Table 10. This table shows that Bristol Bay scales, on the average, have five adjacent circuli that are substantially wider than on scales from fish of other geographical areas. This feature is found on scales of Bristol Bay salmon of all freshwater ages. Krogius and Krokhin (1956) also have noted variation in spacing of circuli.

Aleutian Islands to Cook Inlet (Plate 5; Tables 4 and 5)

The area from Chignik to Cook Inlet is an area of high production of Alaskan sockeye salmon, usually second to that of Bristol Bay. To provide a comparison with other areas, the commercial catch in 1966 of sockeye salmon in the subsections of this geographic area are shown below (International North Pacific Fisheries Commission, 1966):

Area	*Thousands of fish*
Aleutian Islands	1.0
South side Alaska Peninsula	606.2
Chignik	222.1
Kodiak Island	631.6
Cook Inlet	1,866.5

Commercial fishing operations in the Aleutian Islands and along the south side of the Alaska Peninsula take both transient fish migrating to Bristol Bay and local stocks (Atkinson, 1955). My samples from the Aleutian Islands, obtained for INPFC purposes, are of local stocks.

TABLE 10.—Frequency tabulations of the width of the widest five adjacent circuli in the first ocean zone of age 1. sockeye salmon from representative areas.[1] (Asterisks indicate modes.)

Width[2]	Asia[3]	Bristol Bay	Chignik	Cook Inlet	Fish Creek	Ketchikan	Skeena River	Rivers Inlet	Fraser River	Columbia River
13	--	--	--	--	--	--	--	1.5	--	--
14	--	--	--	--	--	0.5	--	5.9	0.3	--
15	--	--	--	0.3	--	1.5	0.9	12.4	2.8	0.3
16	--	--	0.3	0.9	0.3	6.5	5.4	20.6	8.3	1.5
17	--	--	1.4	2.9	2.7	16.5	12.2	25.9*	13.2	4.9
18	0.9	--	4.0	7.6	6.1	23.0*	16.8	20.0	16.7	11.0
19	3.2	0.2	9.1	13.1	9.1	20.0	19.0	8.8	18.4*	14.6
20	6.0	0.6	16.8	17.7	13.7	12.5	19.3*	2.9	16.7	15.2
21	8.8	2.0	21.3*	20.1*	18.0	8.5	15.1	0.9	12.1	16.8*
22	12.5	4.7	18.5	17.7	18.6*	5.5	7.1	0.3	6.6	15.5
23	15.7	7.8	12.5	10.8	14.0	2.0	2.3	0.6	2.8	11.3
24	16.7*	12.0	7.7	4.4	7.9	1.5	1.4	0.3	1.1	6.1
25	16.2	15.7	4.8	2.0	4.3	1.5	0.6	--	0.6	1.8
26	12.0	17.3*	2.8	1.2	2.7	0.5	--	--	0.3	0.6
27	5.6	15.7	0.9	0.6	1.8	--	--	--	--	0.3
28	1.9	10.9	--	0.6	0.6	--	--	--	--	--
29	0.5	6.3	--	0.3	--	--	--	--	--	--
30	--	3.5	--	--	--	--	--	--	--	--
31	--	1.8	--	--	--	--	--	--	--	--
32	--	1.1	--	--	--	--	--	--	--	--
33	--	0.4	--	--	--	--	--	--	--	--
No. in sample	54	281	88	80	82	50	88	85	87	82

[1] All samples from 1963 except Ketchikan, 1964.
[2] Millimeters of projected image, magnification 82X.
[3] Asian samples from an area near Southeastern Kamchatka coast where Asian fish are present almost exclusively (Margolis, Cleaver, Fukuda, and Godfrey, 1966). Data smoothed according to Henry (1961).

In the Aleutian Islands a number of scale types may be found. One type from Attu Island is similar to that of Asian fish: a small freshwater zone with few, often broken and irregular circuli. The first ocean zone of these Attu fish has evenly spaced, often broken circuli, but usually fewer circuli than the Asian fish. Another type, found in Unalaska Island samples in some years, has a larger freshwater zone with more circuli, like Bristol Bay fish (see submode at 17-18 circuli in column 8 of Table 4). A third type in both Adak and Unalaska Islands (see column 7 and primary mode in column 8 of Table 4) samples, has a large freshwater zone with numerous circuli like the Fish Creek sockeye salmon (these are pictured in Plate 8). Fish from Adak Island tend to have fewer circuli in the first ocean zone than fish from other areas. As noted above, the numbers of fish produced in the Aleutian Islands are very small, consequently these scale types are included here only to provide a complete series of age 1. scales.

Scales from Chignik, Kodiak Island, and most streams in Cook Inlet have moderately small freshwater zones with relatively few circuli (except those from Fish Creek, Plate 8), often with plus growth. Generally most of the fish from Kodiak Island are of ages 2. and 3. The first ocean zone of the fish from Chignik to Cook Inlet has a few more circuli on the average than do scales from Bristol Bay fish; moreover, the circuli are closer together and more uniformly spaced. The position of the widest circuli, if present, varies considerably in fish of this area group but often is near the following winter zone like many of the Asian fish.

Copper River to Southeastern Alaska (Plate 6; Tables 4 and 5)

The Copper River is the only river of significant production of sockeye salmon in this large geographical area; however, there are many streams that provide small numbers of fish to make a substantial total. The commercial catch for 1966 for subdivisions of this area follow (International North Pacific Fisheries Commission, 1966):

Area	*Thousands of fish*
Copper River	1,005.6
Yakutat	184.4
Southeastern Alaska	868.7

Fish of age 1. predominate here every year. Most fish from these areas are quite similar in both freshwater and first ocean circuli. The freshwater zone is small with few circuli. The freshwater zone of many fish taken near Petersburg and Ketchikan is very small with very few circuli, similar to that of the Rivers Inlet fish, but there are differences in the first ocean zone that distinguish Rivers Inlet scales. Most freshwater circuli of all fish of these areas are broken, irregular, crowded together, and poorly marked. Some scales show plus growth.

The first ocean zone of fish from these areas has a few more circuli on the average than do scales from Chignik or Cook Inlet. Circuli are usually irregular but evenly spaced; generally there is no area of wider circuli but sometimes there are a few wider circuli in two or more places in the first ocean zone. Adventitious checks (false winter marks) may also be present in the ocean zones. Thus some of these scales may be difficult to use for determination of age and racial origin.

British Columbia and the Columbia River (Plate 7, Tables 4 and 5)

This is also an area of high production of sockeye salmon. The yearly total for British Columbia varies, but it is either first or second to Bristol Bay in the total for North America. Average catches (from Aro and Shepard, 1967) for the major areas of British Columbia are as follows:

Area	*Millions of fish*
Nass River (average 1951-1963)	0.21
Skeena River (average 1951-1963)	0.49
Rivers and Smith Inlets (average 1951-1963)	1.06
Fraser River (average 1938-1963):	
1901 cycle	2.87
1902 cycle	6.12
1903 cycle	1.73
1904 cycle	1.92

Relatively few sockeye salmon are produced in the Columbia River (see Table 1). Fish of age .1

predominated in all sections of this geographical area; however, in some years age 2. fish may be abundant in the Nass River.

Most scales of fish from the rivers identified in this plate do not differ much between areas. (Scales from sockeye salmon from Rivers and Smith Inlets and some from the Nimpkish River are distinct and are shown on Plate 9.) Freshwater zones on the scales of fish from the Nass and Skeena Rivers tend to have slightly fewer circuli, and those from the Columbia River slightly more circuli than those from the Nimpkish and Fraser Rivers. (Scales from sockeye salmon from the Nimpkish River which are represented by the primary mode in column 20 of Table 4 are not pictured here as they are similar to the scales of Fraser River fish.) The freshwater circuli of scales from fish of these areas are mostly regular and unbroken. These characters give the freshwater zone a clear-cut appearance. Plus growth is often present.

The first ocean zone is usually distinct and well marked. There are numerous circuli in this zone, and even if some of them are irregular or broken, the zone usually has a clear-cut appearance. The spacing of circuli tends to be uniform, but a few wider spaced circuli may occur at any position within the zone. Scales from the Nimpkish River tend to have the most circuli of any of these areas. Adventitious marks are common in the ocean zones, but in spite of these irregularities, the circuli and winter marks are generally distinct and easy to count and measure.

Geographical Areas with Distinctive Scale Types (Plates 8 and 9)

There are two types of scales showing this freshwater age which are distinctive:

1. The "Fish Creek" type (Plate 8), so called because it was first observed in Fish Creek, Knik Arm, Cook Inlet, but later also found in small numbers in some other streams as noted below .
2. The "Rivers Inlet" type (Plate 9), so called because it was first observed in Rivers Inlet, B.C., but later found in some other areas, also noted below.

Fish Creek Type (Plate 8; Tables 4 and 5).— Fish Creek type scales are on most sockeye salmon from Fish Creek. A few were also found in the samples from Adak and Unalaska Islands and in the recently available samples from Frazer Lake (Kodiak Island) and the Nimpkish River (fish with more than 20 circuli in column 20, Table 4).

Fish Creek type scales are characterized by a large freshwater zone with many well-marked circuli. There is often a check or winter mark about 18 or 20 circuli from the center of the scale, followed by a few circuli of plus growth.

The circuli of the first ocean zone are also well marked, and in most cases, well separated, sometimes with an area of wider spaced circuli near the freshwater zone like most of the Bristol Bay fish. The numbers of circuli in this zone tend to vary with the locality from which the fish came: Adak and Unalaska Island, less than 22 circuli; Fish Creek and Kodiak Island, 22-27 circuli; and the Nimpkish River, over 27 circuli.

The annual number of adult fish with this scale type from all areas is relatively small (perhaps in the neighborhood of 100,000 fish as a maximum), but the scales have been observed in offshore samples because of their distinctive appearance (Mosher et al., 1961).

Rivers Inlet Type (Plate 9; Tables 4 and 5).— Gilbert (1914) first noted that scales of sockeye salmon from Rivers Inlet and later from Smith Inlet were different from those of other areas. Recently, samples from the Nimpkish River (on Vancouver Island, which empties into the northern end of Johnstone Straits near Rivers and Smith Inlets) became available. Some of these scales were also of the Rivers Inlet type.

These scales are characterized by a small, diffuse freshwater zone with very few circuli. Usually the circuli are broken, irregular, crowded together and difficult to count. The transition from freshwater to ocean growth is usually diffuse and difficult to distinguish.

The first ocean zone, the distinctive feature of these scales, has many uniformly spaced circuli, usually with no area of wider spacing. This first ocean zone often looks like freshwater

growth of scales from other areas (compare these photographs with those of the Fish Creek type on Plate 8). The second ocean zone is of typical ocean growth—heavy textured, well-spaced circuli. This zone, unlike that on scales from other areas, is usually wider than the first ocean zone. Often the winter check between the first and the second ocean zones is diffuse and indistinct.

The whole scale shows two large areas of contrasting texture: the freshwater and first ocean zones of fine-textured circuli and the second and subsequent ocean zones with coarse-textured circuli of typical ocean growth. On the scales from fish of other areas there is a difference in texture, but the zone of fine texture, the freshwater growth, is relatively small; and the coarse-textured portion of the scale, the entire ocean growth, is the major portion of the scale.

In the Nimpkish River, some of the fish of this age have scales of Rivers Inlet type (secondary mode at 12 circuli in column 20 of Table 4). These fish generally have a few more circuli in both the freshwater and first ocean zones than the fish from Rivers Inlet, and the circuli are also usually less broken and irregular than those from Rivers Inlet. The difference in texture, however, between the first and second ocean zone is typical of Rivers Inlet type scales.

Most of the fish from Rivers and Smith Inlets have scales of this type. In representative samples the following typical Rivers Inlet scales were found:

(Area and year)	*Percentage of Rivers Inlet type*
Rivers Inlet, 1958	126 of 156 fish (76.2%) (Manzer, Bilton, and Mosher, 1960)[7]
Rivers Inlet, 1963	374 of 377 fish (98.4%)
Smith Inlet, 1960	123 of 132 fish (93.2%)
Smith Inlet, 1961	246 of 270 fish (91.1%)

These percentages approximate the range of typical Rivers Inlet type scales in this area. The few scales that are not typical of fish of these areas usually resemble scales of the Skeena or Nass Rivers; consequently they still are in British Columbia.

Only an occasional scale from the other areas (Cook Inlet to the Fraser River) has the appearance of a Rivers Inlet scale. In these few cases, the number of circuli in the first ocean zone is usually less than that of the Rivers Inlet fish.[8]

In a test of 300 unlabeled scales from many areas over the range of the species set up by an assistant, I correctly identified 63 out of 64 Rivers Inlet scales. This indicates that these scales are indeed distinct and can be identified from their appearance with a high degree of accuracy.

The Rivers Inlet area is a good producer of sockeye salmon. In most years more than 1 million fish are caught there. The Nimpkish River is a small producer, but escapements of 150,000 and 70,000 fish were recorded in 1957 and 1958, respectively (Henry, 1961).

Rivers Inlet type scales have been observed widely in offshore samples (Manzer et al., see footnote 7; Mosher et al., 1961).

AGE 2., ASIA (Plate 10; Tables 6 and 7)

Representative scales of sockeye salmon from the Kamchatka, Ozernaya, and Bolshaya Rivers, the Okhotsk Sea, and Lakes Blizhnee and Dalnee are shown on this plate. Like those of age 1., scales from these fish, except Lakes Blizhnee and Dalnee, do not differ much between areas. The freshwater zone is of moderate size, sometimes with plus growth. The circuli are close together and many are broken or irregular. (See Table 9 for a summary of freshwater scale characters of Asian sockeye salmon from Krogius, 1958.)

The first ocean zone of scales from these fish also do not differ significantly and are similar to the same zone of the scales of the age 1. fish from the same areas. Usually the circuli are evenly and moderately closely spaced and lack the open

[7] Manzer, J. I., T. H. Bilton, and K. H. Mosher. 1960. The ocean distribution of sockeye salmon originating in Rivers and Smith Inlets. Fish. Res. Board Can. (Nanaimo, B.C.) and Bur. Commer. Fish. (Seattle, Wash.) (INPFC Doc. 407), 5 p. (Processed.)

[8] From this point on, the term "Rivers Inlet" also includes Smith Inlet and the Rivers Inlet type scales of fish from the Nimpkish River.

appearance of the Bristol Bay scales. An area of wider spaced circuli may often be found at any position in the first ocean zone, but usually it is near the middle of the zone or the following winter zone. Plus growth is sometimes present.

Scales of many fish from Lake Blizhnee are distinctive. They have a very small freshwater zone with few circuli in each year's growth. Circuli are irregular and the zone is difficult to interpret because of the broken and closely spaced circuli. The first ocean zone is similar to that of the other Asian fish of the Ozernaya, Bolshaya, and Kamchatka Rivers.

Scales from Lake Dalnee fish have large to very large freshwater zones. The freshwater growth makes up a larger portion of these scales than those from any other locality over the range of the species. The circuli of both the freshwater and ocean zones are usually regular and well marked. Sometimes there are fewer circuli in the first ocean zone than on scales from other Asian areas. Scales of fish of this freshwater age can be easily identified as being from Lake Dalnee when they are encountered in samples of fish taken from the North Pacific and Bering Sea because of the unusually large freshwater zone (Mosher et al., 1961).

AGE 2., NORTH AMERICA

Bristol Bay (Plate 11; Tables 6 and 7)

The number of fish of this freshwater age varies from year to year in the different rivers, but few are ever found in the Nushagak and Togiak areas. In some years of large production in Bristol Bay most of the fish are of age group 2.2.

As was true of age 1. fish from Bristol Bay (Plate 4), most scales from these fish, including Bear River, do not differ much between streams. Freshwater and ocean circuli are regular and clear cut. The freshwater zone is moderately large to large, and well marked; the circuli are generally well separated, and plus growth is often present. There are relatively few, well-separated circuli in the first ocean zone. In most cases the winter marks are distinct. Usually the widest circuli are near the freshwater zone. Because the first 5 or 10 circuli of each ocean growth zone usually are widely separated and the winter marks are well marked and compact, the scales have a more open appearance than scales of fish from other geographical areas. Taken as a whole, scales from Bristol Bay fish are easier to interpret than sockeye scales from other geographical areas.

Aleutian Islands to Cook Inlet (Plate 12; Tables 6 and 7)

Fish of age 2. are usually abundant in this area. Diverse types are present. Aleutian Islands (typified by Attu Island) and Chignik River fish have a small freshwater zone with irregular circuli much like the Asian sockeye salmon. Fish from Unalaska Island (not pictured), Red River (Kodiak Island), and Cook Inlet have moderate-sized freshwater zones with more irregular and broken circuli on their scales than Bristol Bay fish, but fewer than the Asian fish. Adak Island and Karluk River (Kodiak Island) fish have large, usually clear-cut, freshwater zones on their scales, also with more irregular circuli than those from Bristol Bay.

As is true with the age 1. fish, Adak Island sockeye salmon have the fewest circuli in the first ocean zone of their scales; those from Unalaska Island have about the same distribution of circuli as the Bristol Bay fish; and those from Attu Island and from the Alaska Peninsula to Cook Inlet have somewhat more circuli than fish from Bristol Bay. The circuli in the first ocean zone are generally closer together than on scales from Bristol Bay fish. The area of widest circuli, if present, may occur at any position within the growth zone, but it is often near the following winter ring, such as occurs with many Asian fish. Many of the scales from this area, especially from the Aleutian Islands and Chignik, are difficult to interpret with confidence.

Copper River to Columbia River (Plate 13; Tables 6 and 7)

In this large area relatively few age 2. sockeye salmon are produced. In fact only in some years in the Nass River are there substantial numbers.

There are, however, a number of different scale types among those that do occur.

Most fish from the Copper River, Yakutat, and Petersburg areas have scales much like those of Chignik and Cook Inlet. The scales are characterized by small- to medium-sized freshwater zones in which most of the circuli are broken or irregular. The first ocean zone of these scales averages slightly more circuli than those of the Cook Inlet area, however, and the circuli are more closely and evenly spaced.

A second type of scale from this area has a large freshwater zone with numerous circuli. These scales are found in small numbers in various areas from the Copper River to the Columbia River and are shown in Plate 14.

Scales showing this freshwater age from the Nass, Skeena, and Fraser Rivers and some from the Nimpkish River (the British Columbia fish) usually have moderately large, well-marked freshwater zones. Usually the broken circuli are confined to the winter checks. In the first ocean zone, fish from the Nimpkish River have more numerous, regular, evenly spaced circuli than those from any other area. Scales of these British Columbia fish are relatively easy to interpret and often differ from Bristol Bay scales only in having, on the average, a few more circuli and more evenly spaced circuli in the first ocean zone. The scales tend to have a less open appearance than those of Bristol Bay fish.

The few scales of this age group of sockeye salmon from the Ketchikan area occur in at least three types: (1) scales like those of the Copper River-Petersburg area, like the one pictured on this plate from a fish taken near Petersburg, (2) scales with a larger freshwater zone like those from Nass River fish, and (3) very few scales with very large freshwater zones like the one pictured from the Copper River on Plate 14. In the Ketchikan area there are many small streams that produce some sockeye salmon. In addition, many channels and bays serve as waterways through which fish migrate to other areas. Thus it is possible that many of the Petersburg and Nass type scales taken in this area may actually be from fish migrating to the Petersburg area or the Nass River.

Most fish of this age found in the Columbia River have large freshwater zones varying from those like the one pictured on this plate to ones with very large freshwater zones, shown on Plate 14. On all of these Columbia River scales, the freshwater circuli are well marked and well separated, even if many are broken or irregular. The circuli of the first ocean zone of these scales are also usually well marked; they are evenly and widely spaced. The zone averages somewhat fewer circuli than on scales from the Nimpkish, Nass, Skeena, and Fraser Rivers but more than on the scales from Bristol Bay fish. An area of wider spaced circuli may occur at any position within the first ocean zone, but the difference between the widely spaced and the closely spaced circuli is not as great as in the Bristol Bay scales.

Fish of this freshwater age are rare in Rivers Inlet. These scales can be identified as typical Rivers Inlet type from their appearance (see Plate 14).

Areas with Some Distinctive Scales (Plate 14)

In most years a number of areas from Kodiak Island to the Columbia River have some fish with very large freshwater zones on their scales, but except for the Nimpkish River, there were not enough fish to provide data for frequencies of the number of circuli. Only slight differences in the freshwater zone of the fish from the various areas can be found.

In some years, scales from some Bristol Bay and Aleutian Island fish may also have these very large freshwater zones.[9] These are not pictured on this plate because they resemble the ones shown from the Copper River to the Columbia River, and they do not occur in most years.

Differences in the number and character of the circuli in the first ocean zone of the scales from fish of the different areas, however, offer an indication of the locality from which the fish came. The largest number of circuli in this zone tends to be on scales of the Nimpkish River sockeye salmon; fewer circuli (and more broken

[9] A number were observed in Bristol Bay samples for 1970.

circuli) are found on the scales from Ketchikan, Petersburg, Copper River, and Columbia River fish; even fewer circuli (and fewer broken circuli) are found on the Fish Creek and Kodiak Island fish, whereas the least number of circuli (and the most complete and regular circuli) are found on the scales from Aleutian Island and Bristol Bay fish.

The reasons for some of the fish from these areas having such a large freshwater growth zone is a subject for future research. The numerous streams and tributaries of the larger river systems encompass a wide range of environmental conditions. It is likely that these fish are spawned and grow in nursery areas with excellent conditions for freshwater growth. In some years the growth conditions in certain streams may be better than in other streams, contributing to the year to year variation in numbers of fish with this scale type.

In Rivers Inlet, sockeye salmon with scales showing this age are rare. The scales of the few fish that have been found, however, are of typical Rivers Inlet appearance: a small freshwater zone with only a few (mostly broken) circuli in each year's growth, a fine-textured first ocean zone with numerous circuli, and a second (and subsequent) ocean zone of typical ocean type circuli. Thus the scales show the two large areas of contrasting texture, like those of Rivers Inlet scales of other ages—Plates 1 and 9. (Note how much the scale area to the end of the first ocean zone, white arrow, resembles the freshwater zone of the Columbia River scale on this plate.)

AGE 3., ASIA (Plate 15; Tables 8a and b)

Usually fish of this freshwater age are in substantial numbers only in the Asian areas and in Kodiak Island streams, but a few are also found each year in Bristol Bay, especially in the Egegik and Naknek Rivers.

On the Asian side of the Pacific Ocean, scales from fish of the Ozernaya, Bolshaya, and Kamchatka Rivers and the Okhotsk Sea do not differ much (column 1 of Table 8 shows data from fish taken off the southeast coast of the Kamchatka Peninsula where a number of Asian stocks intermingle). The scales of most Asian fish, except those from Lakes Blizhnee and Dalnee, have relatively small freshwater zones with only a few circuli in each year's growth. Many of the circuli are irregular, broken, and closely spaced. The first ocean zone of these scales is like that of the age 1. and 2. fish from the same geographical areas. There are a few more circuli present on the scales of these fish than on those from Bristol Bay, and the circuli are generally uniformly spaced. An area of wider spaced circuli may be present in the first ocean zone, but it generally is less pronounced than on scales from Bristol Bay fish.

Fish of this age are also found in Lake Blizhnee. The scales have a very small freshwater zone with very few circuli in each year's growth. The first ocean zone of these Lake Blizhnee fish is also like that of the other Asian fish except those from Lake Dalnee.

Fish of this freshwater age are relatively common in Lake Dalnee. The scales are distinctive: a very large freshwater zone with numerous, usually clear-cut circuli. The freshwater zone makes up a larger portion of the scales of fish from Lake Dalnee than of fish from any other area in Asia or North America. As in age 2. and 4. fish, the first ocean zone often had fewer circuli than usual for Asian fish—sometimes even fewer than on scales from Bristol Bay or Adak Island fish.

AGE 3., NORTH AMERICA (Plate 16; Tables 8a and b)

As noted above, Kodiak Island has the most sockeye salmon of age 3. on the American side of the Pacific Ocean. In some years a major portion of the run to the Karluk River may be of individuals of this freshwater age with 2 or 3 winters in the ocean (the 3.2 and 3.3 ages). In most years substantial numbers of age 3. fish are found. The freshwater zone of the scales of these fish is relatively large; the circuli are well separated and usually well marked, although more of the circuli may be irregular or broken than on most Bristol Bay scales. The first ocean zone is also well marked; the circuli are distinct and often widest near the freshwater zone as in

the scales of fish from Bristol Bay. Usually a few more circuli are found than on Bristol Bay or Asian scales.

Bristol Bay scales of this age (Egegik River shown) look like Bristol Bay scales of age 2. with an additional freshwater winter mark. The freshwater zone is moderately large and distinct; the circuli are well marked. Circuli of the first ocean zone are also distinct and are fewer in number than on scales from fish of other North American areas except Adak Island. The circuli are usually widely separated near the freshwater zone. These scales, like those from fish of the other Bristol Bay age groups, are usually easy to interpret.

Fish of this age are rarely found in other North American areas. Scales from these age 3. sockeye salmon resemble those of age 2. from the same area but have an additional winter mark in the freshwater zone. Thus, usually the freshwater zone is large (Nimpkish River shown). In Chignik and southeastern Alaska (Petersburg shown) where small freshwater zones predominate, occasionally a fish with a very small freshwater zone with three distinct winter marks may be found.

Among fish of this age, the number of circuli in the first ocean zone is similar to that of age 1. and 2. fish from the same area; thus the number of circuli in the first ocean zone can indicate the area of origin of the fish.

AGE 4., ALL AREAS (Plate 17)

Scales that show this age are rare from Asia to Cook Inlet, Alaska, and are almost never observed in areas southeast of Cook Inlet. Insufficient numbers of fish of this age group have been obtained to assemble frequency distributions of the number of circuli on the scales of fish from any area. While it is possible that some of these scales may be younger with accessory checks, the spacing and appearance of the markings suggests that most of them are actually age 4.

It appears from the scales which I have seen that the freshwater and ocean zones are similar to those found on scales of fish of age 2. and 3. from the same geographical areas, with additional winter marks in freshwater, and consequently somewhat larger freshwater zones. For instance, the scales of fish from Lake Dalnee have an enormous freshwater zone, and relatively few circuli in the first ocean zone. The Lake Blizhnee fish of this age, on the other hand, have scales with a small freshwater zone with relatively few circuli in each year's growth and with approximately the same number of circuli in the first ocean zone as would be found in most Asian fish of age 2. or 3.

Fish of the Aleutian Islands show two different types of scales. One type (similar to Lake Blizhnee scales) has an extremely small freshwater zone with few circuli in each year's growth. Scales of this type have broken and irregular circuli in both the freshwater and ocean zones, as on the scales of many Asian fish. They average fewer circuli in the first ocean zone than Asian fish, however, and often average fewer circuli than on scales from Bristol Bay fish. The second type, illustrated by a scale from Adak Island, is similar to scales of fish of the same age in Bristol Bay (Egegik River shown). The freshwater zone is moderately large with numerous circuli, some of which are irregular or broken. The first ocean zone has circuli like scales of age 2. fish from the same locality. Generally the circuli are well marked and more widely spaced near the freshwater zone.

Scales from Kodiak Island (illustrated by scales from Karluk River and Frazer Lake) have freshwater zones that vary from large to extremely large.

DETERMINATION OF ORIGIN OF SOCKEYE SALMON TAKEN IN OFFSHORE WATERS

This section is not a formal key for classifying sockeye salmon by stock or geographic origin. The purpose of this section is to show how age and scale characteristics illustrated in the previous section of the paper can be used by experienced workers to assist in identifying the most probable area of origin of many sockeye salmon taken in offshore waters.

Scales of fish from different offshore areas re-

quire different considerations for study. The following discussion is divided into two parts for purposes of racial identification of the fish:

1. The area westward of long 175° W in the North Pacific Ocean and Bering Sea.
2. The eastern North Pacific Ocean and Gulf of Alaska.

WESTERN AND CENTRAL NORTH PACIFIC AND BERING SEA

Studies of the distribution of sockeye salmon stocks in central North Pacific and Bering Sea for the INPFC, including the morphological, parasitological, and tagging reports noted in the introduction, as well as the scale studies of Mosher (1963) and Mason (1966, 1967a, 1967b) have shown intermingling of stocks primarily from Asia and Bristol Bay over most of the offshore area westward of long 175° W to between 160° and 170° E, depending on the latitude (see Figure 74 of Margolis et al., 1966).

When examining scales of fish from this area, occasionally a scale with a very large freshwater zone may be seen. These scales usually stand out distinctly from others and are most likely from Lake Dalnee fish (Plates 3, 10, 15, and 17). A few scales, however, may be seen with unusually small freshwater zones. These scales are most likely from fish from Lake Blizhnee (Plates 3, 10, 15, and 17).

Aside from these scales with unusually large or small freshwater zones, nearly all of the scales are of two types: (1) Bristol Bay type scales (Plates 4, 11, 16, and 17)—well-marked scales with regular circuli in all growth zones and a moderately large freshwater zone, usually with less than 23 circuli in the first ocean zone. The widest spacing of circuli in the first ocean zone (and often the other ocean zones as well) is usually near the freshwater zone. The ocean portion of these scales has an open appearance. (2) Asian type scales (Plates 3, 10, 15, and 17)—relatively small freshwater zones with many broken or irregular circuli. The first ocean zone usually has 23 to 26 circuli which are widely spaced over the whole summer growth portion but lack the open appearance of the Bristol Bay scales. The ocean zone of these fish often has three and sometimes four winter marks.

EASTERN NORTH PACIFIC OCEAN AND GULF OF ALASKA

When we examine scales of fish taken eastward of long 175° W and in the Gulf of Alaska, many types may be encountered. At the present state of knowledge, I believe that determination of origin is extremely difficult or impossible if separation by each individual stream or river within the area is required. If, however, determination by general locality of origin and certain areas is the immediate goal, age and scale characteristics can be used to classify many, if not most, of the fish.

No sockeye salmon tagged in the Gulf of Alaska has ever been returned from Asian coastal streams.[10] Numerous sockeye tagged in other areas and other species tagged in the Gulf of Alaska have been returned from Asian coastal rivers. Considering that many thousand sockeye salmon have been tagged in the Gulf of Alaska, at least a few should have been recaptured from Asian waters if any Asian fish were present there during the time of tagging.

Thus, the Asian stocks need not be considered when dealing with fish taken in the Gulf area. Some of the scales of fish taken from the Alaska Peninsula eastward to southeastern Alaska resemble Asian fish in some characters at least. This similarity to Asian fish in scale characters has been noted by Oseko (1961),[11] and in morphological characters, by Fukuhara et al. (1962). Consequently any scales encountered in the Gulf of Alaska samples that resemble those from

[10] One fish tagged at 48°29′ N, 159°10′ W in the area south of the Gulf of Alaska in 1961 was recovered the same year off the Kamchatka coast at 50°47′ N, 162°29′ E. Kondo et al. (1965) concluded that it was not possible to draw any definite conclusions from the recovery. Margolis et al. (1966), however, considered it a Kamchatka sockeye salmon.

[11] Oseko, M. 1961. Certain characteristics of the growth pattern of scales as a means of discriminating between sockeye salmon from various streams of Alaska and the Kamchatka Peninsula. [In Japanese.] Hokkaido Reg. Fish. Res. Lab. (INPFC Doc. 479). 38 p. of Japanese text; 5 p. of preliminary English translation. (Processed.)

Asian fish can be considered of North American origin and classified accordingly.

In the area east of long 175° W into the Gulf of Alaska, the number of circuli and the general appearance of the freshwater and first ocean zones of most scales of age 1. fish can be evaluated and the most probable area of origin can be determined by comparison with the scales in Plates 4 to 7.

Rivers Inlet scales can be identified easily by their appearance. They stand out distinctly from the scales of other areas in all freshwater ages because of the fine-textured circuli of the freshwater and first ocean zones (Plates 1, 9, and 14).

Some scales may be found that have large freshwater zones. In age 1. these are most likely from Unalaska or Kodiak Island, Fish Creek, or the Nimpkish River (Plate 8). In age 2., they may be from Kodiak Island, Fish Creek, Copper River, the Ketchikan area, the Nimpkish, Fraser, or Columbia Rivers (Plate 14). None of these stocks are abundant in these ages, but some are taken at times. The number of circuli in the first ocean zone may assist in determining from which specific area the fish originated.

Migration routes to the various streams have not yet been determined for most stocks, but certain indications are given by tagging studies. Research by the Canadians for the INPFC (Fisheries Research Board of Canada, 1967a, 1967b) shows that fish recovered in the Rivers Inlet-Fraser River area tend to have been tagged farther southward in the Gulf of Alaska in spring and summer than those recovered from the Cook Inlet and Copper River areas. Fish recovered from Bristol Bay tend to have been tagged farther westward than those recovered from the Rivers Inlet-Fraser River areas. Hartt (1962, 1966) and Kondo et al. (1965) indicated that many Bristol Bay fish move westward along the south side of the Alaska Peninsula and the Aleutian Islands, turn north through the passes, and then migrate eastward into Bristol Bay.

Thus if the scale (age 2.) under study has a large freshwater zone and a large number of circuli in the first ocean zone (over 27 circuli) and was taken in the southern part of the Gulf of Alaska, it would be most likely from the Nimpkish River (Plate 14). If the scale had 23 to 27 circuli in the first ocean zone and was taken in the northern part of the Gulf, it would probably be from Cook Inlet, Kodiak Island, or Fish Creek; if it had 28 to 30 circuli, it would probably be from the Copper River or southeastern Alaska (Plate 14); and if it had less than 23 circuli, it would probably be from a Bristol Bay fish (Plate 11), or possibly from a spawning stream on Adak or Unalaska Island (Plate 12)) if caught near the Aleutian Islands.

In age 3. sockeye salmon, a scale with a large freshwater zone and about 26 circuli in the first ocean zone indicates most likely a Kodiak Island fish; less than 23 circuli, Bristol Bay or Unalaska Island origin; and over 30 circuli, Nimpkish River origin (Plate 16). A scale with a very small freshwater zone and 25 to 28 circuli in the first ocean zone indicates a fish probably from the Copper River or southeastern Alaska (Plate 16).

In age 0. fish, aside from the Rivers Inlet fish which are distinguishable by their compact, fine-textured first ocean zone (Plate 1), the number of circuli in the first zone offers the best indication of area of origin: a few circuli (20 to 25), Bristol Bay; a large number (over 34), southeastern Alaska southward; or an intermediate number (26 to 34), the area from Bristol Bay to southeastern Alaska (Plate 1).

In age 4., any fish found in the Gulf of Alaska will most likely be from Kodiak Island (Plate 17). If the scale is from a fish taken near the Aleutian Islands and has relatively few circuli in the first ocean zone, it may be from a stream on Attu or Adak Island (Plate 17) or from Bristol Bay.

South of lat 50° N in the southern Gulf of Alaska, the intermingling of stocks may be complex. Very few fish have been tagged in this area; catches are very small as a rule, and consequently little is known about these fish. Study of their scales offers the best means of identifying their origin and determining other features of their life history.

Evidence from fishing by United States, Japanese, and Canadian research vessels south of lat 50° N in the late autumn, winter, and early spring indicated that sockeye salmon of many stocks may be present over a wider area to the

southward than during May and June when most fishing has been carried on.[12]

Kondo et al. (1965) show the estimated area of distribution of sockeye salmon in May and June. In the area between long 165° and 175° W, they show only Bristol Bay and Gulf of Alaska stocks (not quite to 170° W). Thus in the area between long 170° and 175° W, probably only Bristol Bay (Plates 1, 4, 11, 16, and 17), Alaska Peninsula, and Aleutian Island stocks (Plates 5, 12, 16, and 17) will be present in most years.

These procedures have been the result of intensive study of sockeye salmon scales from 1954 to 1971. In addition I have examined collections taken before 1954 (Bristol Bay, from the early 1920's; Karluk River, from the mid-1940's; Copper River, from the mid-1930's; the Petersburg area, from the late 1940's; and the Columbia River, selected years from 1910 to 1922) and have verified the scale characters pictured and described here. Although there are minor differences from year to year, within and between areas, the characters have been relatively stable over a long period of time. The pictures of Rivers Inlet scales shown in Gilbert (1914) resemble the Rivers Inlet sockeye salmon scales of recent samples. Thus the pictures and descriptions shown in this report are representative of scales from fish of these areas and can be used as guides in determining the racial origins of fish taken in offshore areas of the North Pacific and adjacent seas.[13]

[12] I have examined the few scale samples available from the area south of lat 50° N and eastward of long 175° W and have observed many diverse scale types. This leads me to believe that fish from many sources intermingle there: some fish from Bristol Bay, the mainland areas around the Gulf of Alaska, and even from Asia.

[13] Study of salmon scales, in common with other fish scales, is a specialized branch of fishery biology. It requires a person with a special temperament: one who can sit in a darkened room, often for hours at a time, involved in routine counting and measuring of scale features. It requires a person who can evaluate the subtle differences between scales and not be overcome by them. Consequently, a sympathetic approach and a certain amount of experience with fish scale study is required to be able to use scale characteristics to determine the racial origins of sockeye salmon. When a scientist has obtained this experience and can evaluate the differences among scales, he will find that the information available through study of the scales can be applied toward answering many questions of the life history of the individual fish in addition to its age and racial origin.

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APPENDIX TABLE 1.—Commercial catch of sockeye salmon, 1964 to 1968.

Area	1964	1965	1966	1967	1968
			Thousands of fish		
Asia	8,143.5	13,677.2	8,817.5	10,753.6	8,966.7
Japan	7,175.0	12,171.0	7,667.0	9,783.0	8,131.0
USSR	968.5	1,506.2	1,150.5	970.6	835.7
North America	14,135.7	34,115.8	20,496.8	17,513.6	15,343.4
Canada (B.C.)	3,619.0	3,019.4	4,020.3	6,743.0	6,266.0
United States	10,517.7	31,096.4	16,476.5	10,770.6	9,007.4
North of Bristol Bay	13.4	12.9	1.1	1.3	5.9
Bristol Bay	5,825.7	24,718.7	9,559.5	4,555.4	3,030.0
Alaska Peninsula	1,427.3	1,857.2	1,460.9	1,074.0	2,341.7
Cook Inlet	990.7	1,424.4	1,866.5	1,406.6	1,124.1
Copper River Area	780.0	946.0	1,131.1	568.2	797.2
Southeastern Alaska	923.9	1,085.3	1,054.1	971.5	830.8
Washington & Oregon	556.7	1,050.9	1,403.3	2,193.6	947.7

Source of data: International North Pacific Fisheries Commission, 1964-68, and from Supplemental data provided to the INPFC by the USSR.

DEVELOPMENT AND EARLY LIFE HISTORY OF THE NORTHERN SENNET, *Sphyraena borealis* DeKAY (PISCES: SPHYRAENIDAE) REARED IN THE LABORATORY[1, 2]

EDWARD D. HOUDE[3]

ABSTRACT

Eggs and larvae of the northern sennet, *Sphyraena borealis* DeKay, are described from laboratory-reared specimens. Fertilized eggs were collected on the edge of the Florida Current near Miami in December 1969. Larvae were 2.6 mm SL (standard length) at hatching and 13.5 mm SL at 21 days after hatching. Head and snout length increased rapidly relative to standard length as larvae grew. A fleshy tip developed on the lower jaw when larvae were longer than 5 mm SL. Teeth also first appeared at about 5 mm SL. Myomere and vertebral numbers were constant at 24. Ossification of the axial skeleton began in the cephalic region and proceeded caudad as growth occurred. Fin ray complements were complete at about 13.5 mm SL. Pigmentation during development is described and illustrated. Behavior of laboratory-reared *S. borealis* larvae is discussed. Several wild-caught postlarvae were used to extend the descriptive series and helped to validate the identification of the laboratory-reared larvae.

Little is known about early development of barracudas (Sphyraenidae) in the Western Atlantic Ocean. Larvae of the northern sennet (also called northern barracuda), *Sphyraena borealis* DeKay, recently were reared in the laboratory, and the eggs, yolk-sac larvae, and early postlarval stages are described in this report from a series of preserved specimens, providing the first description of this species in its earliest life stages. De Sylva (1963) described some postlarval *S. borealis* and presented keys to identify the postlarvae of western North Atlantic sphyraenids longer than 5.5 mm SL (standard length).

Some confusion exists regarding the systematic relation of *S. borealis* and the similar *S. picudilla* Poey (southern sennet). The two species are regarded by de Sylva (personal communication) as valid species, separable on minor morphometric characters in adults. Briggs (1958) reported *S. borealis* to be distributed nearshore from Bermuda and Massachusetts to Panama, including the north central Gulf of Mexico. Adults of *S. borealis* from southern Florida intergrade in many characters toward those of *S. picudilla* (de Sylva, personal communication). Postlarvae reared in the laboratory during this study always closely resembled the *S. borealis* described by de Sylva (1963).

The eggs and yolk-sac larvae of *Sphyraena argentea* Girard from the eastern Pacific were described by Barnhart (1927). Orton (1955) also described *S. argentea* eggs and yolk-sac larvae as well as older larvae of about 4 and 7 mm TL (total length). Eggs and young larvae of *S. pinguis* Günther from the western Pacific were described by Shojima, Fujita, and Uchida (1957), and their development was reviewed by Uchida et al. (1958). Development of *S. sphyraena* Linnaeus collected in the Mediterranean was summarized by Vialli (1956), and illustrations of some stages were presented by Lo Bianco (1956). Development of *S. barracuda* (Walbaum), commencing with postlarval stages, was discussed by de Sylva (1963). Except for the material on *S. sphyraena*, complete developmental series appear to be lacking for barracudas. My specimens of *S. borealis* provide a

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complete series of egg and larval development of this species. In addition to the reared specimens, some postlarvae and juveniles of *S. borealis* were collected in nets, helping to extend the series beyond the lengths of the longest specimens reared in the laboratory.

MATERIALS AND METHODS

REARING TECHNIQUES

Pelagic eggs of *S. borealis* were collected in a 1-m, 505-μ mesh plankton net at the sea surface in the Florida Current, about 8 km east of Miami Beach on December 11, 1969, at 10:00 AM EST. Surface temperature was 23.6° C at time of collection. A total of 78 eggs were isolated from the catch. They were incubated and the larvae reared in a 55-liter aquarium. Temperature ranged from 23.2° to 24.5° C and salinity from 33.0 to 34.6‰ during the experiment. Larvae were fed zooplankton collected from Biscayne Bay and nauplii of brine shrimp (*Artemia salina*). Some pelagic fish eggs were added to the rearing tank beginning the 7th day after hatching to provide newly hatched fish larvae as a food source for the sennets. Constant illumination was provided to allow the larvae to feed continuously, both by day and night. Many details of methods used to rear fish larvae were described by Houde and Palko (1970).

PRESERVATION OF LARVAE

Only a small series of eggs and larvae were obtained during development because of the small number (78) of eggs available. Two eggs and 18 larvae were preserved in 5% buffered Formalin during the 23 days of the rearing experiment.

WILD-CAUGHT POSTLARVAE AND JUVENILES

Plankton collections in the Florida Current near Miami Beach between January 13 and January 27, 1970, provided 10 postlarval and young juvenile specimens of *S. borealis* from 7.4 to 30.6 mm SL. In addition, two juveniles, 59.6 and 62.9 mm SL, were collected from Biscayne Bay in a 20-ft beach seine in January 1970. These wild-caught specimens provided data to extend the descriptive series and helped to validate the identification of the laboratory-reared larvae as *S. borealis*.

MERISTICS AND MORPHOMETRICS

Fin rays and spines were enumerated for each of the fins. Myomeres (preanal plus postanal) were counted on each larva when they could be distinguished.

The following measurements were made:

Total length (TL): tip of snout to tip of caudal fin.

Standard length (SL): tip of snout to tip of notochord or, in more developed larvae, to base of caudal rays.

Body depth: height of body, exclusive of finfold, at base of pectoral fin.

Head length: tip of snout to posterior margin of otic capsules in yolk-sac larvae and tip of snout to opercular margin in postlarvae.

Snout length: tip of snout to anterior margin of the fleshy orbit.

Preanal length: tip of snout along midline to vertical from anus.

Eye diameter: horizontal distance from anterior to posterior margin of the fleshy orbit.

Tip of lower jaw: length of fleshy extension on tip of lower jaw.

1st predorsal length: tip of snout to anterior insertion of spinous dorsal fin, measured along the body midline.

2nd predorsal length: tip of snout to anterior insertion of second dorsal fin, measured along the body midline.

All counts and measurements were made using a binocular dissecting microscope and ocular micrometer.

OSTEOLOGY

Six larvae, 7.4 to 17.0 mm SL, were cleared with trypsin and stained with alizarin (Taylor, 1967) to determine the sequence of ossification and to accurately assess the lengths at which fin

rays first develop. A complete study of osteology was not undertaken, but development of teeth and caudal skeleton were examined in detail.

DEVELOPMENT

EMBRYO

Two preserved eggs of *S. borealis* were 1.22 and 1.24 mm diameter. They had single, clear yellow oil globules 0.27 and 0.29 mm diameter. The perivitelline space was narrow and the transparent yolk was vaguely segmented. In eggs that I preserved about 2 hr after collection, the embryo was not well developed and no pigment was visible (Figure 1A). Later stage embryos developed both melanophores and xanthophores on the body, giving the living embryo a greenish appearance to the naked eye. The eggs hatched about 20 hr after collection at an incubation temperature of 24° C.

MORPHOLOGY OF LARVAE AND JUVENILES

Larvae of *S. borealis* were 2.6 mm SL at hatching and were robust due to the large yolk sac (Figure 1B) but became characteristically slender after its absorption (Figures 2 and 3). Body depth averaged 12% SL for larvae from immediately after yolk absorption to juveniles of 21.0 mm SL. Gut length was moderately long in *S. borealis* larvae. Jaws were not elongated on newly hatched larvae but became so shortly after the yolk sac was absorbed and mouth parts became functional. Growth in length of laboratory-reared larvae is given in Figure 4.

Yolk Absorption

The yolk sac was large and nearly spherical at hatching, with its oil globule at the anterior end (Figure 1B). Some yolk and the oil globule remained up to 4 days after hatching (Figures 2A and 2B). Feeding began shortly before the yolk was completely absorbed.

Head Length

The head of recently hatched *S. borealis* was short (Figures 1 and 2), but increased rapidly in length as larvae developed. Head length increased relative to body length from 13% SL for newly hatched larvae to a constant value of about 33% SL for larvae 9 mm SL and longer (Table 1). Over half the head length increase was related to an increase in length of the snout during development.

Snout Length

Snout length increased on developing larvae from about 3% SL 1 day after hatching to a value of about 12% SL at 9 mm and gradually to 14% SL for juveniles (Table 1).

Tip of Lower Jaw

A fleshy tip began to develop on the lower jaw at about 5.0 mm SL (Table 1). Its relative length increased from less than 1% SL to about 3% SL when larvae had grown to 14.5 mm SL (Figures 2 and 3). The structure ranged from 3 to 6% SL on 17 to 30 mm SL wild-caught specimens. On two juveniles, 59.6 and 62.9 mm SL, the length of the fleshy tip was only 3% SL. The length of this structure on both laboratory-reared and wild-caught specimens varied rather markedly.

Jaws and Teeth

The mouth was not developed until larvae were 4.0 mm SL, about 3 days after hatching (Figure 2B). Teeth first appeared on the premaxillary bones at 5.3 mm SL when the jaws became barracuda-like (Figures 2C and 2D). Initially, the teeth appeared bluntly conical but became caninelike when larvae grew to 7.0 mm SL. Teeth were developed on the lower jaw and were developing on the palatine bones at 7.4 mm SL. The palatine bones on larvae longer than 12 mm SL bore the largest teeth, except for the second and third pairs of premaxillary teeth; these were long and directed posteriorly. All

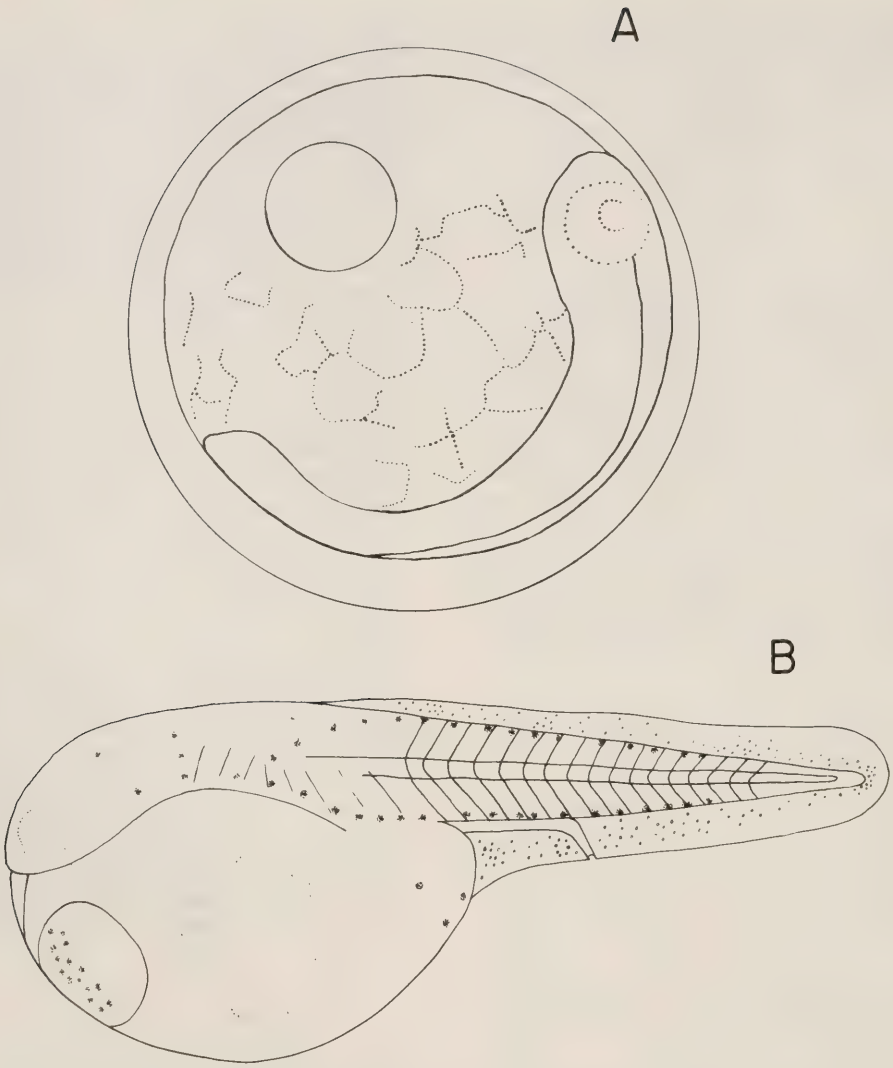

FIGURE 1.—Embryo and newly hatched larva of *Sphyraena borealis*. A. Embryo; B. Newly hatched larva, 2.6 mm SL. Inclusions in the finfold are not pigment.

teeth were strong and caninelike; most were slightly curved and directed backward at their tips. The number of premaxillary teeth increased from 4 at 5.3 mm SL to about 20 at 21.5 mm SL. Lower jaw teeth increased from 11 at 9.4 mm SL to about 15 on specimens from 12.1 to 21.5 mm SL. Palatine teeth numbered 6 at 9.4 mm SL and increased to about 10 at 21.5 mm SL.

Eye Diameter

Eye diameter decreased slightly, from 8% SL on newly hatched larvae to 7% SL for most individuals longer than 16.9 mm SL (Table 1).

Myomeres

The number of myomeres was constant at 24 (14 preanal plus 10 postanal) throughout development.

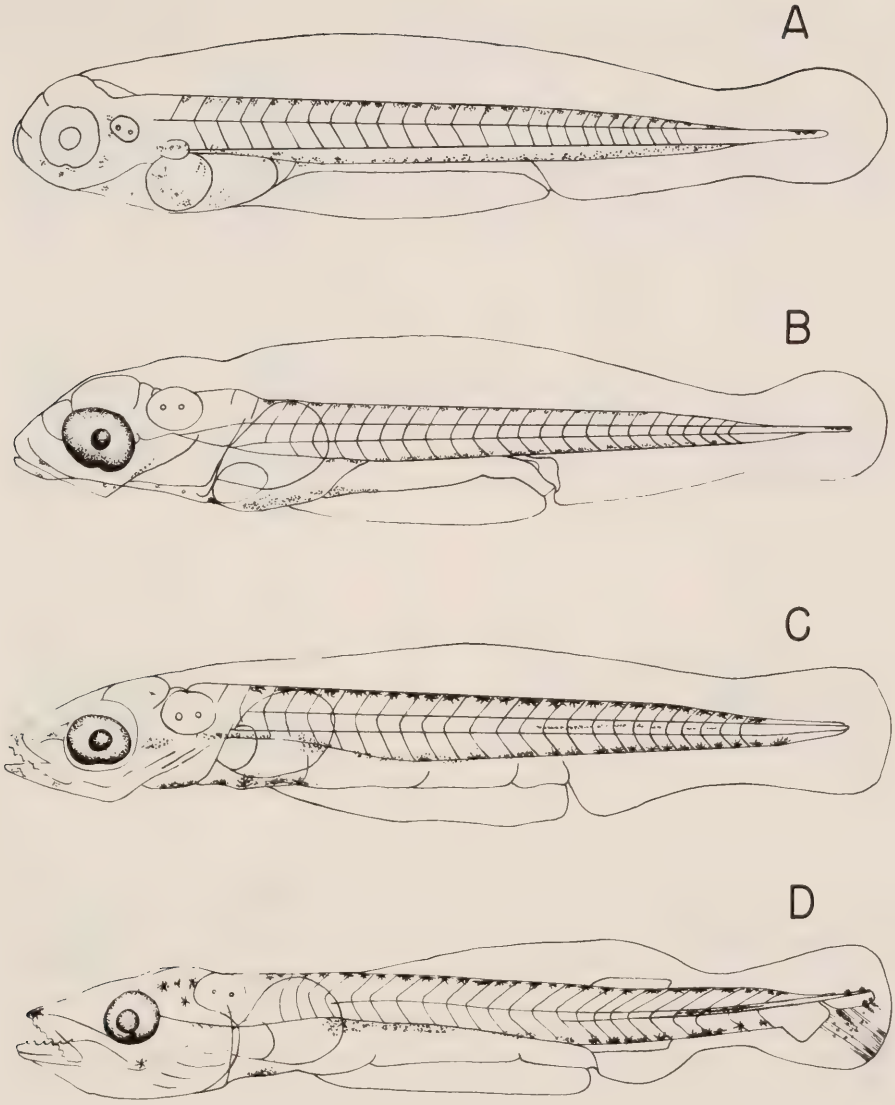

FIGURE 2.—Developmental stages of *Sphyraena borealis* reared in the laboratory. A. 3.8 mm SL; B. 4.3 mm SL; C. 5.3 mm SL; D. 7.4 mm SL.

Keeled Scales

Keeled scales appeared along the lateral line on the caudal peduncle when specimens were about 14.5 mm SL (Figure 3C).

Osteology

Ossification of the axial skeleton proceeded from the cephalic region caudad as growth occurred. A 7.4-mm SL specimen appeared to have nearly complete skeletal development of the head region, but little development posteriorly. Vertebral development was restricted to incomplete neural and haemal arches in the 7.4-mm SL larva. Centra were forming in a 9.1-mm SL larva and appeared to be completely developed

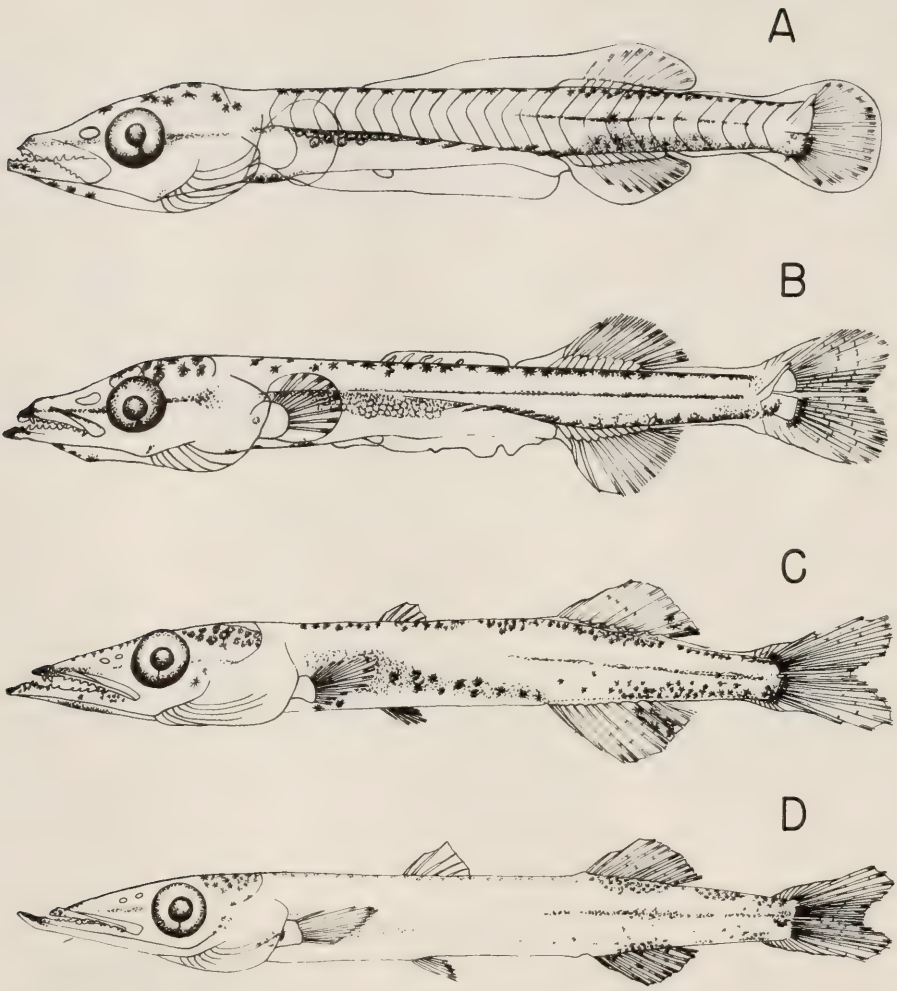

FIGURE 3.—Developmental stages of *Sphyraena borealis*. Specimens A, B, and C were laboratory reared; specimen D was collected in a plankton net. A. 9.4 mm SL; B. 12.3 mm SL; C. 14.5 mm SL; D. 21.0 mm SL.

in a 10.9-mm SL larva. All specimens had 24 vertebrae.

Six branchiostegals were present on the 7.4-mm SL larva and a seventh had developed on the 9.1-mm SL specimen. Cleithra were present but poorly ossified at 7.4 SL; they were well developed at 9.1 mm SL.

Ossification of the caudal region began at 7.4-mm SL. At this size, the hypural bones were developing and some rays could be distinguished in the ventral half of the caudal finfold. All caudal elements were beginning to develop by 10.9 mm SL and were easily recognized on a 12.1-mm SL specimen. The last three vertebrae (including the urostyle) contributed to support of the caudal fin; both neural and haemal spines of the antepenultimate vertebra (22nd) supported developing accessory rays of the caudal fin, as did the haemal spine of the penultimate (23rd) vertebra. A total of 6 hypural bones

TABLE 1.—Summary of morphometric data from laboratory-reared (L) larvae and from wild-caught (W) larvae and juveniles of *Sphyraena borealis*. (Specimens between broken lines are undergoing notochord flexion.) Except for total and standard lengths, measurements are proportional values, the ratio of the character relative to standard length.

Specimen No.	Total length	Standard length	Preanal length	1st predorsal length	2nd predorsal length	Head length	Snout length	Tip lower jaw	Eye diameter
	mm	*mm*							
3 (L)	2.6	2.6	0.68	--	--	0.13	--	--	--
4 (L)	4.0	3.8	.66	--	--	.14	0.03	--	0.08
5 (L)	4.2	4.1	.63	--	--	.19	.04	--	.08
7 (L)	4.3	4.2	.56	--	--	.19	.04	--	.08
6 (L)	4.5	4.3	.66	--	--	.21	.05	--	.08
9 (L)	5.2	5.0	.65	--	--	.26	.07	<0.01	.08
10 (L)	5.5	5.3	.67	--	--	.26	.07	<.01	.08
8 (L)	5.8	5.6	.68	--	--	.27	.08	<.01	.07
11 (L)	7.7	7.4	.66	--	--	.28	.10	<.01	.07
27 (W)	7.9	7.4	.71	--	--	.30	.12	.02	.08
12 (L)	9.5	9.0	.69	--	0.67	.31	.12	.01	.08
13 (L)	10.2	9.4	.70	--	.68	.32	.13	<.01	.09
14 (L)	12.2	10.9	.70	--	.68	.33	.14	.02	.08
17 (L)	12.9	11.3	.71	0.50	.70	.36	.12	--	.08
15 (L)	13.4	11.9	.69	--	.68	.31	.13	.02	.08
18 (L)	13.7	12.1	.69	.44	.68	.33	.12	.01	.08
16 (L)	13.7	12.3	.66	.44	.66	.32	.13	.03	.08
19 (L)	14.7	12.7	.68	.47	.70	.34	.13	.02	.08
24 (W)	15.9	13.7	.72	.49	.71	.32	.12	.05	.07
23 (W)	16.5	14.4	.72	.48	.70	.36	.15	.04	.08
20 (L)	16.7	14.5	.63	.47	.71	.35	.14	.03	.08
28 (W)	19.4	16.9	.70	.47	.70	.33	.14	.04	.07
26 (W)	19.1	17.0	.69	.48	.70	.32	.14	.04	.06
30 (W)	19.7	17.1	.70	.46	.70	.32	.13	.04	.06
29 (W)	21.2	18.4	.70	.47	.70	.33	.14	.05	.07
21 (W)	24.2	21.0	.71	.49	.72	.34	.15	.06	.08
25 (W)	24.6	21.5	.70	.46	.69	.32	.14	.03	.07
22 (W)	33.9	30.6	.70	.46	.70	.32	.14	.06	.07
32 (W)	66.8	59.6	.71	.46	.70	.32	.14	.03	.06
31 (W)	70.0	62.9	.72	.45	.71	.32	.14	.03	.06

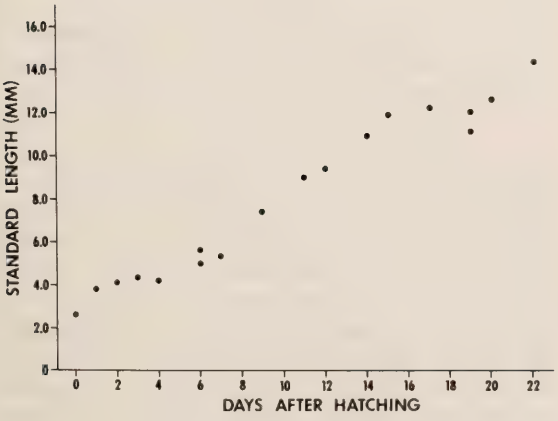

FIGURE 4.—Growth of *Sphyraena borealis* larvae reared in the laboratory at an average temperature of 24.0° C.

were formed near the posteroventral surface of the urostylar vertebra. There were 3 epurals and 2 pairs of uroneurals ossifying dorsal to the urostyle. The 17 principal caudal rays were supported by the hypural bones. Principal caudal ray support was as follows: hypural 1 supported rays 1 to 3; hypural 2 supported rays 4 to 7; hypural 3 supported ray 8; hypural 4 supported rays 9 to 11; hypural 5 supported rays 12 to 15; hypural 6 supported rays 16 and 17. A 17.0-mm SL specimen differed from smaller specimens only in having the first principal caudal ray partially supported by the haemal spine of the penultimate vertebra as well as the first hypural bone. All elements were at least partially ossified at 17.0 mm SL; both the epurals and uroneurals were the most poorly ossified bones of the caudal skeleton at this stage. Hollister (1937) examined caudal skeletons of adult and

TABLE 2.—Summary of meristic data (spines and rays) from laboratory-reared (L) and wild-caught (W) larvae of *Sphyraena borealis*. (Dashes indicate elements were present but could not be accurately counted.)

Specimen No.	Standard length	Principal Caudal rays	Anal fin	2nd dorsal fin	1st dorsal fin	Pelvic fin		Pectoral fin	
						Left	Right	Left	Right
	mm								
3 (L)	2.6	0	0	0	0	0	0	0	0
4 (L)	3.8	0	0	0	0	0	0	0	0
5 (L)	4.1	0	0	0	0	0	0	0	0
7 (L)	4.2	0	0	0	0	0	0	0	0
6 (L)	4.3	0	0	0	0	0	0	0	0
9 (L)	5.0	0	0	0	0	0	0	0	0
10 (L)	5.3	0	0	0	0	0	0	0	0
8 (L)	5.6	0	0	0	0	0	0	0	0
27 (W)	7.4	0	0	0	0	0	0	0	0
11 (L)	7.4	7	0	0	0	0	0	0	0
12 (L)	9.0	16	8	8	0	0	0	0	0
13 (L)	9.4	16	9	9	0	0	0	0	0
14 (L)	10.9	17	10	10	3	0	0	0	0
17 (L)	11.3	17	11	10	5	5	--	8	6
15 (L)	11.9	17	11	10	3	--	--	--	--
18 (L)	12.1	17	11	10	5	--	--	8	8
16 (L)	12.3	17	11	10	4	5	--	8	6
19 (L)	12.7	17	10	10	5	--	--	10	--
24 (W)	13.7	16	11	10	--	5	--	12	12
23 (W)	14.4	17	--	10	5	5	6	--	12
20 (L)	14.5	17	11	10	5	--	6	12	10
28 (W)	16.9	17	11	10	--	--	--	--	--
26 (W)	17.0	17	11	10	5	6	6	11	12
30 (W)	17.1	17	10	10	5	--	--	--	--
29 (W)	18.4	17	11	10	--	--	--	--	--
21 (W)	21.0	17	11	10	--	--	--	--	--
25 (W)	21.5	16	11	10	5	6	6	12	12
22 (W)	30.6	17	11	10	5	6	6	12	12

juvenile *S. borealis*, *S. picudilla*, and *S. barracuda*. She found that all were similar and showed that a progressive fusion of caudal elements occurred in barracudas as they grew. Fusion of hypurals 2 and 3, 4 and 5, and of the urostyle with hypural bones was apparent in her large specimens.

Fin Development

Newly hatched larvae had a prominent larval finfold (Figures 1 and 2) that appeared granular because of many bubbles or small inclusions distributed throughout. These inclusions were not illustrated, except in the newly hatched larva (Figure 1B), but were present until larvae grew to about 9.5 mm SL.

Fin ray development essentially was completed at 13.5 mm SL (Table 2). Fan-shaped pectoral fins without rays developed at 3.8 mm SL 1 day after hatching (Figure 2A). Rayed fins developed in the following sequence: caudal, anal and second dorsal, first dorsal, pelvics, and pectorals. The caudal fin rays began to develop at 7.4 mm SL when the notochord started to flex (Figure 2D). All 17 principal caudal rays were present on a 10.9-mm SL larva. Accessory caudal rays (raylets) also were developing at 10.9 mm SL. Their number varied from 6 to 8 dorsally and 6 to 9 ventrally on specimens up to 30.6 mm SL. The anal and second dorsal fins were represented only by opaque areas in the finfold at 7.4 mm SL, but rays of these fins were developing at 9.0 mm SL; posteriormost rays developed before the more anterior rays and 9 rays were present in each fin at 9.4 mm SL (Figure 3A). A full complement of 2nd dorsal (I, 9) and anal (I, 9 or 10) elements was present at 10.9 mm SL. Spines of the first dorsal fin appeared at 10.9 mm SL and a full complement of 5, located over vertebrae 5 to 7, was present on a 12.1-mm SL larva. The 5 spines were more heavily ossified and located over vertebrae 6 to 8 on a 17.0-mm SL specimen. Pelvic fin buds formed on larvae as small as 9.4 mm SL, but rays did not begin to develop until 11.3 mm SL. Pectoral fin rays also began to develop at this length. All pelvic (I, 5) and pectoral (12) elements were not present on

all larvae until about 13.5 mm SL. Remnants of the larval finfold persisted until 12.5 mm SL (Figure 3B).

Pigmentation

Except where specifically mentioned, references to pigment are to melanophores. Xanthophores were common on larvae, and both silver iridophores and blue chromatophores were present. (See Fujii, 1969, for chromatophore terminology.) Some variations in melanophore patterns were present among *S. borealis* larvae of similar size but the following description gives the typical sequence of development.

Melanophores and xanthophores were present on newly hatched larvae but the latter faded after preservation. Small melanophores were distributed in a dorso-lateral and ventro-lateral row on each side of the larva (Figure 1B). The two rows converged just above the yolk sac and ran anterior as a single row to the posterior cephalic region, joining a series of melanophores located over the hindbrain. Other melanophores were present on the anterior half of the oil globule and near the posterior of the yolk sac.

One to two days after hatching (about 3.8 mm SL), melanophores became larger and more numerous (Figure 2A). Those located in the lateral rows and on the cephalic region became stellate. They were more numerous on the yolk sac and two small melanophores appeared near the developing mouth. A series of two to six small, contracted melanophores were noted near the tip of the notochord. The eye became pigmented at 2 days after hatching.

As larvae developed, both melanophores and xanthophores became more numerous. Xanthophores were distributed over much of the body and consisted of elongate yellow cells forming a loose network on the body. In life, larvae appeared green because of the presence of both yellow and black pigments. Blue iridophores on the hindgut and some iridescent pigment in the eyes also were present.

By 7 days after hatching (about 5.3 mm SL, Figure 2C) stellate melanophores had appeared over the brain, on the tip of the upper jaw, lower jaw, angle of the jaw, ventral margin of the opercular region and over the foregut. Each dorso-lateral row of stellate melanophores was well developed while the ventro-lateral rows were condensing into a single ventro-medial row, posterior to the anus. A mid-lateral series of melanophores was developing posterior to the anus.

At 9 days after hatching (about 7.4 mm SL) pigmentation became more intense (Figure 2D). About 5 melanophores were present in the developing caudal fin. The fleshy tip of the lower jaw began to become darkly pigmented on some specimens at this stage. The extent and intensity of pigmentation continued to increase on older larvae (Figures 3A and 3B). No changes in pattern were observed, except for development of a line of pigment that bisected the eye, and a migration of melanophores from the tip of the developing urostyle to the ventral margin of the hypural plate.

When specimens were 20 to 22 days old (about 12.5 to 14.5 mm SL), the juvenile pattern of dorsal and lateral blocks of pigment began to appear (Figure 3C). Stellate melanophores also developed in the second dorsal and anal fins of individuals of this size. Longer specimens from plankton collections had the typical juvenile pigment pattern (Figure 3C) (cf. de Sylva, 1963; Figure 4).

GROWTH AND MORTALITY

Larvae of *S. borealis* grew most rapidly during the first 14 days after hatching, but more slowly during the next 7 days (Figure 4). Larvae were 2.6 mm SL at hatching, averaged 5.5 mm SL at 7 days after hatching, 11 mm at 14 days, and about 13.5 mm at 21 days. The decrease in growth rate of the sennets during the third week may have been caused by the scarcity of fish larvae in their diet. Average growth rate during the rearing experiment was about 0.5 mm per day.

A total of 78 sennet eggs were incubated but only about 50% hatched. From this small number of hatched larvae, 9 survived until 14 days after hatching, when they had developed most of the characters of juvenile sennets. Mortality in the first 14 days included 11 larvae preserved

for describing larval development. No larvae survived beyond 22 days after hatching, probably because of the inadequate diet.

TRANSFORMATION

Transformation from the larval to the early juvenile stage occurred at about 13.5 mm SL for *S. borealis*. At that size, fin ray development was complete and there were no remnants of the larval finfold. Additional evidence that this size marked the end of the larval period was the occurrence of keeled scales on specimens at 14.5 mm SL and the appearance of juvenile pigment patterns between 12.5 and 14.5 mm SL.

COMPARISONS

Among the four early life history series of barracudas that have been described in the literature, newly hatched larvae of *S. borealis* most closely resemble those of *S. pinguis* from Japanese waters (Shojima et al., 1957; Uchida et al., 1958), except for size at hatching. In both species, the oil globule, at hatching, is located at the anterior end of the yolk mass; neither develop melanophores in the finfold. In contrast, the oil globule is located at the posterior end of the yolk mass in newly hatched larvae of *S. sphyraena* (Vialli, 1956) and *S. argentea* (Orton, 1955) and both have melanophores in the finfold.

Eggs of *S. pinguis* (0.69 to 0.82 mm diameter) were considerably smaller than those of *S. sphyraena* (1.11 to 1.15 mm), *S. borealis* (1.22 to 1.24 mm), and *S. argentea* (about 1.5 mm). It is not surprising that at hatching, larvae of *S. pinguis* were smaller than those of *S. borealis*, measuring 1.75 mm as compared to 2.6 mm. Both species were similarly pigmented at hatching, but differed significantly by 45 and 66 hr. Melanophores were larger and more concentrated in *S. pinguis* larvae than in *S. borealis* at the same stage of development.

Older larvae of *S. borealis* and *S. sphyraena* had similar pigment patterns, but those of *S. sphyraena* had a more developed lower jaw tip. Three-day-old larvae of *S. argentea* from California waters had a distinctive band of melanophores on the tail portion of the body just posterior to the anus that was lacking in *S. borealis*. Postlarvae of *S. barracuda* were described and illustrated by de Sylva (1963). They differ substantially from *S. borealis* in being deeper bodied and having a relatively longer snout. Pigmentation of *S. barracuda* and *S. borealis* larvae between 5.5 and 11.9 mm SL also differs somewhat in its detail.

BEHAVIOR

Newly hatched larvae of *S. borealis* drifted about the rearing tank making only occasional feeble swimming attempts when disturbed. At 2 days after hatching, larvae maintained a horizontal position and began swimming actively with short darting motions. Feeding activity was first observed 3 days after hatching. Sennet larvae usually fed using the *S*-flex behavior previously described for many species of clupeiform larvae (e.g., Rosenthal, 1969; Schumann, 1965). Occasionally, however, a sennet larva would strike at a food organism without first flexing its body and examining the item. Zooplankton organisms less than 100 μ in body width were the initial food of larvae. No stomach analyses were carried out on sennet larvae, but most of the food which was placed in the tank were copepod nauplii and copepodites.

Sennet larvae continued to feed on small zooplankton organisms until 10 days after hatching, even though larger plankton, including fish larvae, and nauplii of brine shrimp were present in the tank beginning 7 days after larvae hatched. At 10 days, large plankton (about 300 to 400 μ body width) was accepted as food, as were some unidentified, newly hatched fish larvae about 2 mm in length. A sennet larva would approach a tiny fish larva, assume an *S*-flex position and dart out at the larva, usually seizing it crosswise. Before swallowing it, a sennet would shake the larva and turn it so that its long axis was parallel to the sennet's alimentary tract. Sennets would swallow fish larvae either head or tail first. Fish larvae were the preferred food of sennets longer than 9 mm SL, but this food was not provided in sufficient quantities to satisfy the sennets. Cannibalism was not observed, but sennets became aggressive toward one an-

other at 11 days after hatching. If size variation had been great or if the sennet larvae had been crowded in the rearing tank, cannibalism likely would have occurred.

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SENSORY FACTORS IN THE SIDE-TO-SIDE SPACING AND POSITIONAL ORIENTATION OF THE TUNA, *Euthynnus affinis*, DURING SCHOOLING

PHYLLIS H. CAHN[1]

ABSTRACT

This study was designed to demonstrate the role of the lateral line sensory system in fish schooling. Groups of 2, 3, 4, and 6 adult *Euthynnus affinis* were filmed during schooling orientation in the presence or absence of transparent partitions between them. When the hydrodynamic field between orienting fish was blocked by the partition, they significantly increased their side-to-side spacing, and changed their diagonal to abeam position ratios so that abeam orientation assumed increased importance. Apparently, hydrodynamic contact is essential for the typical spacing and positional orientation in schooling, and the lateral line, as the water turbulence detector, plays a prime regulatory role.

The primary role of vision for the initial approach and prolonged maintenance of parallel orientation of fish in a school has been well known for many years (Parr, 1927). The accessory role of other sensory systems, especially the acousticolateralis, for maintenance of fish-to-fish distance during schooling, has been implicated by numerous investigators (Breder, 1959, 1965; Cahn, Shaw, and Atz, 1968; and Moulton, 1960), but direct evidence has been difficult to obtain. Breder (1965) showed that the side-to-side spacing of danios in a school (*Brachydanio albolineatus*) is "usually just a little over twice the distance from the side of each fish to the outer edge of the trail of vortices" each generates while swimming. He considered that the fish space themselves so as to "respect these vortices or suffer a considerable reduction in locomotor efficiency". Thus, the sensory system primarily involved in hydrodynamic detection should play a key role in regulation of this spacing. Our work (Cahn, Siler, and Fujiya, in press), and that of Dijkgraaf (1963), strongly implicates the lateral line mechanoreceptors in this function.

In a preliminary report on tuna schooling (Cahn, 1967), it was found that a transparent partition that blocked hydrodynamic contact between orienting fish also resulted in somewhat diminished fish-to-fish attraction, and in changed spacing and positional relationships. Prior to this study, many other investigators of fish schooling tried to separate the sensory components involved, and used transparent plastic and glass boxes, tubes and plates, as well as mirrors (reviewed by Shaw, 1970). Variable results were obtained, with little quantification, except for Shaw's study on *Caranx hippos* (1969), which showed a reduced duration of schooling when the fish were separated by transparent partitions.

The present study quantifies the changes in spacing and positional orientation of the tuna, *Euthynnus affinis* (common name, kawakawa), observed in the earlier report, when transparent partitions blocked non-visual schooling cues. The results strengthen the role of hydrodynamic detectors in control of fish positional relationships and side-to-side distance between fish in a school.

MATERIALS AND METHODS

This work was carried out at the Honolulu Biological Laboratory of the National Marine Fisheries Service, where the facilities are available for experimental studies on scombroid fishes. Special transport containers (Nakamura,

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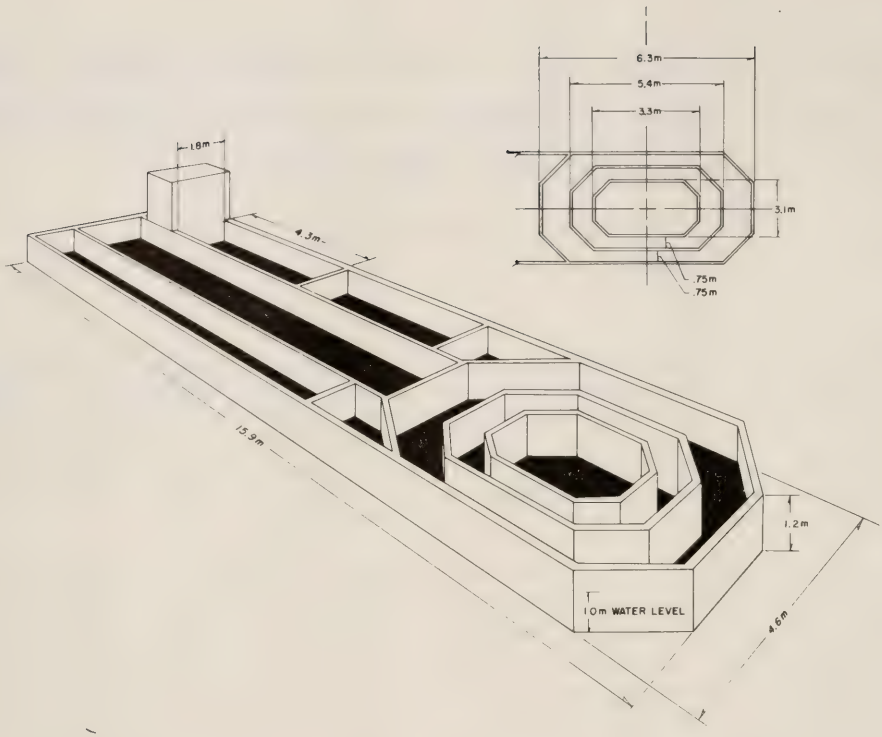

FIGURE 1.—Schematic diagram of cement tank used for tuna schooling studies. Insert shows true dimensions of octagonal channels formed by acetate partitions. Rectangular sidearms were divided in half lengthwise by the Plexiglas partitions, not shown here. Center rectangle was used as a catwalk.

1962) permit the fish to remain in the water from the time of capture until release into tanks on shore.

The experiments were done in a large cement tank that consisted of several differently shaped compartments (Figure 1). An octagonal area at one end was attached by moveable gates (not shown in figure) to rectangular sections at the other end. With the gates up the fish could be transferred to one or the other section without renetting for each experiment. Two concentric octagons of transparent acetate formed three separate swimming compartments for the experimental studies in the octagonal area; in the rectangular areas, rigid, 6.3 mm thick, transparent Plexiglas formed the partitions. The more flexible acetate permitted some hydrodynamic transfer, but the rigid Plexiglas did not. In one series of tests with the Plexiglas partitions, circular holes, 1.25 cm in diameter, were evenly spaced about every 15 cm along the partition.

Films were taken from observation booths at the ends of the sidearms and above the ceiling, over the octagonal area. A 16 mm Bolex was operated at 16 frames per second; a 10 mm Kern-Paillard Switar or a 5.7 mm wide-angle Kinoptic Tegea lens was used. Single frame analysis of selected sequences provided data for quantitative study (L-W Inc. Photo Optical Data Analyzer, Model 224 A, Van Nuys, Calif.). At the film speeds used, it was satisfactory to measure every fifth frame, since positions changed minimally during this time interval. The number of frames given in the tables should

be multiplied by five to reflect the number of frames examined.

Eighteen fish out of 22 adapted to the test conditions; they were tested in groups of 2, 3, 4, and 6, and each fish was used in more than one test. To determine the side-to-side distance between fish that were in parallel orientation, the position of each fish and his body axis were drawn from the motion picture frames. The perpendicular distance between the axes of pairs of orienting fish was measured (Figure 2).

FIGURE 2.—Scale diagram showing tunas swimming without a partition in rectangular channel. The dimensions were taken from a fish of 43 cm fork length. Body axes are shown as dashed lines. The side-to-side distance of 25.9 cm (solid line) is the group mean for a school size of 2 fish.

When occasional non-parallel axes were encountered, the inter-fish spacing was measured from the snout of the leading fish perpendicular to the axis of the trailing fish, or from snout-to-snout if the fish were abeam. The slight body undulations produced while swimming and when each fish turned resulted in slight angular differences in the headings of two otherwise parallel fish. For our purposes it was not necessary to measure these angles, although we spot-checked the first frame of each sequence used to be sure that the angular headings from one another were approximately 26° or less. This was the angular value which Hunter (1968) and Shaw (1969) considered small enough to be counted as parallel fish.

To determine how often two fish in parallel were in an abeam position (directly alongside each other, as in Figure 3), or in a diagonal relationship (alongside, but slightly in front or behind), we scored each frame of the measured sequences as abeam or diagonal, and counted the total number of frames the fish were in these positions. Initially, we measured the diagonal distances to get some idea of how far ahead or behind each other the fish were keeping. At the turns, however, these values became difficult to keep track of. For our purposes, we found it satisfactory to score as diagonal all frames where fish in parallel were more than 5° displaced from a strictly abeam position. We did

FIGURE 3.—Single frame from test on a pair of fish separated by a Plexiglas partition (top of column in Table 2). Upper edge of partition is obscured by reflection from overhead lights. In this frame the fish are about 93 cm apart, just about the mean distance for this test.

not include any frames where fish were in single file formation.

Kawakawa does especially well in captivity (Magnuson, 1965). Young adults were used, of about 37 cm fork length; they had been in holding tanks with running seawater for about 6 months, and appeared normal in all respects. Thawed marine smelts (California osmerids), were fed daily. The water temperature was 23 to 26° C, and was pumped into the tanks at 520 liters/min from a storage sump fed by a well 6 to 9 m deep. The salinity was 33 to 35‰. Dissolved oxygen levels averaged 6 mg/liter. A 1,000 watt and a 300 watt underwater incandescent light, at the bottom of the tank, were used, in addition to banks of overhead fluorescents, to simulate daylight.

RESULTS

In the absence of partitions the diagonal to abeam position ratios for fish orienting in parallel were 5.17/1 and 6.04/1 respectively in the rectangular and octagonal areas. It appeared that the abeam position was assumed for only brief periods when changing speeds in the course of altering direction, turning, or shifting position in the school. In the presence of partitions the ratios were 1.28/1 and 2.36/1 respectively in the rectangular and octagonal areas. Thus the abeam position assumed increased importance during parallel orientation with partitions (Table 1).

The side-to-side spacing is shown in Table 2 as the mean distance apart of either the two fish in a group of two, or of the two closest fish in a group of three or more. Each mean represents measurements made between a single pair of fish during a single continuous film sequence. Without partitions, this distance ranged from 14.0 to 29.8 cm in the rectangular area, and 13.4 to 23.0 cm in the octagonal area. Fish separated by a partition stayed much farther apart; the side-to-side spacing ranged from 64 to 134 cm in the rectangular area (Figure 3), and from 30 to 82 cm in the octagonal area. Fish-to-partition spacing varied from a minimum of about 7 to 8 cm to a maximum of about 75 cm, and appeared to depend on the location of the other fish (Figure 4). Circular holes in the Plexiglas did not change the spacing (Table 2). Water movement through the holes was very slow. Fifteen minutes after fluorescein dye was placed on one side

TABLE 1.—Positional orientation of schooling *Euthynnus*.

	Test area	School size	Total no. frames analyzed[1]	Positions of parallel fish		D/A ratio
				No. frames diagonal (*D*)	No. frames abeam (*A*)	
No partition	Rect.	2	132	110	22	
		3	118	99	19	
		6	96	81	15	
				290	56	5.17/1
	Oct.	2	49	46	3	
		3	44	32	12	
		6	69	61	8	
				139	23	6.04/1
Partition	Rect.	2	360	201	159	
		3	36	25	11	
		4	24	10	14	
				236	184	1.28/1
	Oct.	2	51	36	15	
		3	82	52	30	
		6	52	42	10	
				130	55	2.36/1

[1] These are equal to the number of frames measured for each category in Table 2.

TABLE 2.—Side-to-side spacing of *Euthynnus* in schooling orientation.

Test area	School size	Mean distance apart and standard error					
		No partition			Partition		
		Dist. (*cm*)	SE	No. frames	Dist. (*cm*)	SE	No. frames
Rect.	2	22.0	3.4	(25)	92.4	4.2	(121)
		29.8	2.6	(107)	94.0	2.4	(186)[1]
				132	134.0	5.3	(53)
							360
	3	14.0	0.8	(24)	64.0	6.0	(18)
		17.4	1.0	(94)	90.0	4.4	(18)
				118			36
	6	15.2	0.4	(66)	74.0	2.8	(24)[2]
		16.2	2.4	(30)			
				96			
Oct.	2	19.6	0.6	(22)	30.0	2.1	(21)
		23.0	0.4	(27)	82.0	6.0	(30)
				49			51
	3	20.0	3.0	(21)	48.0	2.8	(27)
		20.0	0.6	(23)	49.5	1.3	(55)
				44			82
	6	13.4	1.0	(27)	42.0	2.2	(30)
		14.8	1.0	(42)	56.0	2.6	(22)
				69			52

[1] This partition contained the series of holes.
[2] There were only 4 fish in this group.

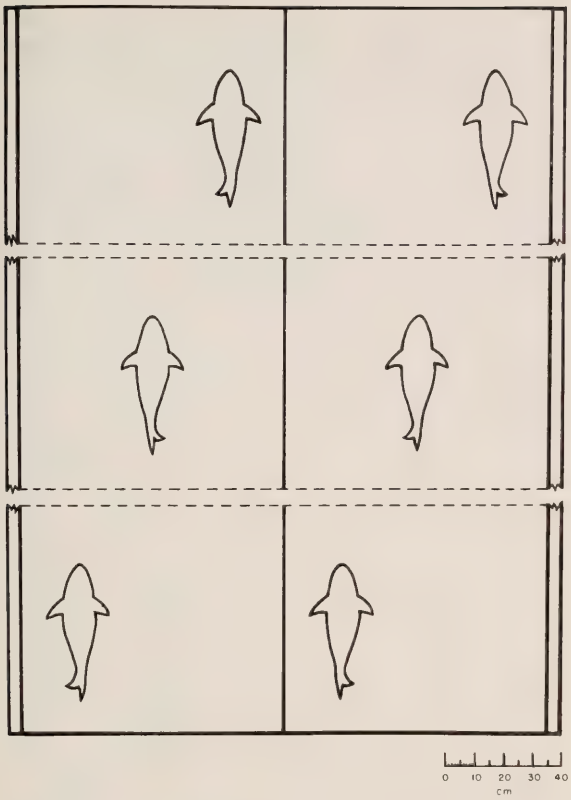

FIGURE 4.—Scale diagrams of tunas swimming with Plexiglas partition in rectangular channel. The 3 usual positions assumed relative to the partition are shown.

the amount that crossed to the other side was barely perceptible.

The data on the side-to-side spacing are summarized in Table 3, where the standard errors were calculated from the variance of the means of the runs in Table 2. It will be noted that in the presence of partitions the variability is much greater. A three-way analysis of variance on the group means (Table 4) showed that the increased spacing in the presence of partitions was highly significant. Although there was a tendency for the fish to remain slightly more compact in the larger groups, these differences were not statistically significant; the effects of shape of the test area was very close to but not quite significant.

TABLE 3.—Summary of data on side-to-side spacing of *Euthynnus* in schooling orientation.

Test area	School size	Group means and standard errors (*cm*)	
		No partition	Partition
Rect.	2	25.9 5.5	106.8 23.3
	3	15.7 2.3	77.0 18.2
	6	15.7 0.7	74.0 —[1]
Oct.	2	21.3 1.8	56.0 36.0
	3	20.0 —[2]	48.7 1.1
	6	14.1 0.9	49.0 9.9

[1] There was only one mean in this case; also only 4 fish in the school.
[2] The two means in this group were the same.

TABLE 4.—Three-way analysis of variance[1] of group means for side-to-side spacing of *Euthynnus*.

Source of variance	Sum of squares	Degrees of freedom	Mean squares	*F* Ratio	Significance level
Total	10,037.42	11			
P or no P	7,440.92	1	7,440.92	44.02	$F_{0.9995}(1,7)=37.0$ $P<0.0005$
Test area	936.94	1	936.94	5.54	$F_{.95}(1,7)=5.59$ not sig.
School size	476.45	2	238.23	1.41	not sig.
Residual	1,183.11	7	169.02		

[1] Fisher, 1970.

Swimming speeds in the absence of partitions ranged from 50 to 64 cm/sec in both rectangular and octagonal areas. With partitions, in the rectangular channels the two orienting fish swam at about the same speed within the range of 50 to 64 cm/sec. During turns, usually made at the ends of the rectangles, they almost always maneuvered to begin the next lap together. Orientation persisted for periods as long as nine days for one pair. In the octagonal area the duration of fish-to-fish orientation was never longer than two days. The size differences between the octagonal channels necessitated differences in swimming speed to maintain fish-to-fish orientation. For example, the fish in the outermost octagon had to swim excessively fast (over 65 cm/sec) to maintain contact with the fish in the innermost section, swimming abnormally slowly (34 cm/sec). Therefore most of the data was obtained in the two larger octagonal channels, where the fish swam at close to normal speeds, at almost 50 to 64 cm/sec.

DISCUSSION

These results demonstrate that blockage of hydrodynamic contact between fish in a school resulted in a significant alteration in side-to-side spacing and a changed ratio of diagonal to abeam positional orientation. Of the various sensory factors of importance in the changes observed, it appears that the loss of acoustico-lateralis cues from neighboring fish played a key role. Some of the alternative explanations are discussed and dismissed below. We did not do any acoustic calibrations; the cement channels and plastic barriers may have caused some resonance of fish swimming sounds, and these may act as orientation cues. But this would assume that the sounds were above the auditory thresholds for these fish, and that the sound can be directionally localized; the latter supposition we can hardly make, as yet, even for other fish whose hearing ability has been extensively studied, with the exception perhaps of goldfish (Moulton and Dixon, 1967). We know nothing about hearing in kawakawa; the yellowfin, *Thunnus albacares*, has moderately good acoustic sensitivity, and also has a swimbladder, an organ that may be helpful for sound pressure to reach the ear (Iversen, 1967). Kawakawa lack a swimbladder; we therefore believe it unlikely that sonic pressure is as important in the lives of these fish as is hydrodynamic particle motion. The latter was blocked by our partitions, so that mate-generated cues to the lateral line mechanoreceptors were obstructed.

There are several hydrodynamic factors to be considered: while it is true that the partitions changed the hydrodynamic field around the fish, and that the solid Plexiglas could possibly cue him to move farther away and thus increase the fish-to-fish spacing, we do not believe this to represent the primary dynamics involved. The increased spacing appeared from our data to represent primarily the fish-to-fish orientation (Figure 4); this orientation resulted in fish moving close to the partition just as often as they moved away from it, while tracking their mates. At all times the fish keep a certain minimal distance of 7 to 8 cm from the barrier, so that we can say that there is some "orientation" to the partition. Superimposed on this is the fish-to-fish orientation, and this exerts the major control of the side-to-side spacing.

Hydrodynamically, when two fish of about the same size are swimming side by side (abeam position) at about the same speed, there would be virtually no centrally located vortices between them. This is because the vortices generated by each fish trail slightly behind him (Rosen, 1959). The flow patterns at the center would, under these conditions, not be very useful as cues. For the fish to get maximal mate-generated hydrodynamic cues it therefore appears that the diagonal positional orientation is preferable. This preference for "diagonal position to each other over positions in front, behind, or directly abeam" was pointed out by Cullen, Shaw, and Baldwin (1965) in their three-dimensional analysis of fish school geometry. Van Olst and Hunter (1970) also called attention to the fact that "the minimum possible lateral space between neighbors to the side would be lower if fish consistently occupied diagonal positions than if they were perfectly aligned, because the areas of tail movement would not overlap." In relationship to our experimental results, the partitions blocked the mate-generated vortices so there was no longer any "advantage" to the diagonal position. The "advantage" factor, it should be emphasized, is not only for hydrodynamic cues from schoolmates, but also more importantly, to derive maximal locomotor efficiency while travelling in a school. The fish can best use the energy from mate-generated vortices if he is positioned within the influence of the vortex, and this is usually best at primarily right angles and a little behind the course of the fish (Breder, 1965), the diagonal position.

Since the fish, in the presence of the partitions, did not completely abandon the diagonal positioning while increasing the abeam orientation, the question comes up of whether or not vision is equally good from both positions? Tuna vision has been studied to a limited extent; for example Nakamura (1968) studied visual acuity in kawakawa by testing the fish's response to various targets. This involved the temporal region of the retina as the fish swam forward towards the target. A different region of the retina is no

doubt involved in lateral vision, with a perhaps different cone distribution. Nakamura did not study this for kawakawa, but others have demonstrated that schooling fish are nearsighted in forward vision but farsighted in lateral vision (Baylor and Shaw, 1962). This suggests that perhaps the kawakawa in our experiments with partitions shifted spacing and position to make more use of lateral vision. A possible reason may be that in the absence of mate-generated hydrodynamic cues, nearsighted vision is inadequate for efficient tracking of their schoolmates. To explain all of these visual factors, more information is needed on such problems as resolution and cone density in the different retinal regions of kawakawa.

One other question relative to vision requires some comment: did the partitions produce reflections sensed by the fish which led to the changes observed? As previously noted, fish in a school in the presence of a partition positioned themselves in different locations relative to the barrier, depending on the fish-to-fish distance across the partition, rather than on the distance from the partition (Figure 4). Thus if there were any reflections, they did not appear to be of any significance. The schooling tendency predominated: relative to this it should be pointed out that it is unlikely that the change in spacing could be attributed, to any major extent, to a waning of the stimulus to school. Fish-to-fish orientation sometimes persisted across the partition for as long as nine days.

We have considered the prime sensory factors, and omitted tactile and chemical contributions. Since these fish rarely touch each other when swimming except under special circumstances of school structure and size (Breder, 1967), there is no need for further concern with the tactile sense. Chemical cues, in our opinion, were probably not transmitted rapidly enough across or through the partitions to be of any consequence. Even with holes in the partitions, as in one series of tests, water-borne transfer was very slow. Also, the part played by chemoreception in fish schooling (McFarland and Moss, 1967; Moss and McFarland, 1970) appears unimportant for obligate schoolers such as tunas and other scombroid forms (the use of obligate here is as in Breder, 1967).

The greater variability noted in the side-to-side spacing in the presence of a partition reflects, in our opinion, what happens when the normal hierarchy of sensory systems is interfered with. The dynamic stability of a fish school depends on feedback from all of the different senses. The partitions disrupted this balance, and although schooling persisted, certain limitations were imposed on the process.

In conclusion, this study suggests that the diagonal fish-to-fish positional orientation and the side-to-side spacing assumed during schooling may be more essential for hydrodynamic detection than for visual cues.

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A PREDATOR-PREY RELATIONSHIP BETWEEN THE LEATHER STAR, *Dermasterias imbricata*, AND THE PURPLE URCHIN, *Strongylocentrotus purpuratus*

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ABSTRACT

During 1969 and 1970, we spent more than 150 hr underwater observing interaction between the leather star, *D. imbricata* and the purple sea urchin, *S. purpuratus*. The majority of the observations were made in shallow (13-15 m) nearshore waters off Pt. Loma, Calif.

The defensive responses exhibited by the purple sea urchin when contacted by the leather star indicated the presence of a well-developed predator-prey relationship. The responses included retraction of sea urchin podia, depression of spines, gaping and erection of globiferous pedicellariae, and usually movement away from the asteroid.

Within the study area off Pt. Loma, 437 feeding leather stars were encountered underwater, and of these, 204 or 47% were eating *S. purpuratus*. In contrast, previously published observations by Mauzey, Birkeland, and Dayton (1968) on the feeding behavior of asteroids off the state of Washington indicated that echinoids were excluded from the diet of *D. imbricata*. We suggest that (1) prey density and availability, (2) search time, (3) taste or gustatory preferences of the sea star, and (4) some form of associative learning by the leather star may be responsible for the variation in the feeding behavior of *D. imbricata* in different areas.

Early laboratory studies by Prouho (1890) and Jennings (1907) described the behavioral responses of sea urchins when encountered by predatory sea stars. More recently, Jensen (1966) recorded the responses of two sea urchin species, *Strongylocentrotus dröbachiensis* and *Psammechinus miliaris*, in the presence of the sea star *Marthasterias glacialis*. Since field observations on the feeding behavior of sublittoral sea stars were rarely made, the laboratory studies only provided the basis for speculation about natural predator-prey interactions between asteroids and echinoids.

Sea urchins might appear to be somewhat immune from predatory attacks by other invertebrate species because they possess such formidable looking armature. However, Mauzey, Birkeland, and Dayton (1968) observed the sea star *Pycnopodia helianthoides* feeding on sea urchins both intertidally and subtidally along the shores of Washington state. Leighton (1971) reported that two species of sea stars, *P. helianthoides* and *Astrometis sertulifera*, feed heavily on juvenile sea urchins. Also, Rosenthal and Chess (1970) identified the leather star, *Dermasterias imbricata* (Grube) as a predator of the purple urchin, *Strongylocentrotus purpuratus* (Stimpson) off San Diego, California.

This paper examines in detail the predator-prey interactions observed between the leather star *D. imbricata* and the purple urchin *S. purpuratus* in both laboratory and field situations. *Dermasterias imbricata* is reported from Prince William Sound, Alaska, to Baja California (Fisher, 1930; Feder, personal communication), while *S. purpuratus* ranges along the Pacific coast of North America from Alaska to Cedros Island, Baja California (Ricketts and Calvin, 1962). Both species occur in intertidal and subtidal situations in cooler temperate climates of the Eastern Pacific; however, south of Santa Barbara, California, the leather star is common only in the sublittoral zone.

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DESCRIPTION OF THE STUDY AREA

The main study site was located approximately 1.5 km offshore from Pt. Loma, California (lat 32°42′N; long 117°16′W). The area is within a stand of giant kelp, *Macrocystis pyrifera*, and the bottom in this vicinity is from 13 m to 15 m deep. The primary observation site encompassed an area about 300 m by 150 m. The sea floor within this area is relatively heterogeneous and is composed primarily of siltstone pavement rocks, rocky outcrops, ledges, and intermittent patches of coarse sand. Vertical relief is generally less than about 2 m. Much of the hard substratum was occupied either by the holdfasts of *M. pyrifera* or by low standing, brown algae such as *Pterygophora californica, Cystoseira osmundacea,* and *Laminaria farlowii.*

METHODS

Emphasis was directed towards observing the organisms under natural conditions in the sublittoral zone; however, laboratory observations were used in addition to those made in the field. Experiments in the laboratory were designed to supplement our field observations, since it allowed us to observe behavioral interactions between *D. imbricata* and *S. purpuratus* over a more continuous period of time. The laboratory portion of the study was conducted at the NMFS Fishery-Oceanography Center, La Jolla, California. Experimental animals were maintained from February through April 1970, in fiber glass water tables which contained circulating seawater. Water temperatures in the aquaria varied from 12° to 17°C during the period of observation.

The field studies are the result of approximately 150 hours of underwater observations made while scuba diving from November 1969 through November 1970. All of the leather stars encountered underwater within the perimeter of the study area were included in the feeding behavior observations. In each case we recorded the size (center of the aboral area to the tip of the longest arm) of the leather star, and noted whether or not it was feeding. It was usually necessary to turn the leather star over in order to make the feeding observation and identify the prey. In situations where the prey was ingested whole by the leather star, we forced the food item out of the sea star's mouth by applying pressure to the aboral and oral surfaces as described in Mauzey et al. (1968). Measurements were made with plastic calipers or rules, and the data were recorded underwater on plastic slates.

Estimates of leather star density were determined by swimming belt transects 4 m wide and 25 m long. Initially, these transect lines were placed haphazardly along the bottom, running either perpendicular or parallel to the shoreline. However, we also placed lines in predetermined locations where leather stars were believed to be more abundant. Size distributions and density estimates of the *S. purpuratus*, which inhabited the study area, were determined by removing all of the visible purple urchins from 16 randomly selected m^2 quadrats. The quadrats were chosen randomly along two 50-m transect lines. One of the transect lines followed a siltstone ledge, and the other was placed perpendicular to the shoreline through a dense stand of giant kelp, *M. pyrifera.* After removal from the quadrats the *S. purpuratus* were placed into plastic bags and carried to the surface for measurement and enumeration.

Three methods were used in an attempt to determine the rate of feeding and the time necessary for a leather star to digest a purple urchin:

(1) A wire mesh cage which covered an area of 4 m^2 was placed over a natural population of at least 50 purple urchins, and four leather stars were introduced as predators into the cage.

(2) Leather stars were marked with numbered disc tags which enabled us to identify and observe individuals over extended periods of time. The tags were attached to the aboral surface of the leather star with a loop of monofilament line. The line was passed through the leather star's epidermis and under the calcareous ossicles using a heavy duty needle. All leather stars were tagged at the sea surface and immediately returned to the bottom.

(3) In the laboratory we placed seven leather stars and 76 purple urchins into a 0.915 × 4.27 m (3 ft × 14 ft) fiber glass water table. The water

table contained circulating seawater approximately 0.3 m in depth. Bricks were scattered around the bottom of the tank to provide the urchins additional substratum and cover. The concentration of leather stars to purple urchins was considerably higher than normally found in the field; however, we felt that the increased number of leather stars might increase our chances to observe predation in the laboratory.

FEEDING BEHAVIOR OF *Dermasterias imbricata*

The widespread distribution of *D. imbricata* along the Pacific coast of North America is partially reflected in its feeding behavior. *Dermasterias imbricata* is an active predator that feeds primarily on benthic invertebrates, although it has been observed feeding on algal and detrital material. In areas containing abundant prey, both motile and sessile in habit, the leather star seems to exhibit a "preference" for the sessile forms, in that sessile species are eaten more often than the motile forms. Asteroid feeding behavior experiments by Landenberger (1968) and Mauzey et al. (1968), showed that the sea star *Pisaster ochraceus* exhibited preferences for sedentary mussels to alternative food items offered them. Paine (1969) suggested that few additional prey species are consumed as long as mussels are available to *P. ochraceus*. Landenberger (1968) also found that *Pisaster giganteus* preferred mussels to four gastropod species which were offered to the asteroids as alternative prey. Additional observations by Rosenthal (1971) indicated that, in nature, *P. giganteus* displayed a preference for prey which was either immobilized or sedentary in habit.

Feder (1959) felt that differences in the diet of *P. ochraceus* were largely dependent on changes in prey availability within each intertidal location. A similar situation appears to exist with *D. imbricata*, at least in those regions where feeding observations have been made. Mauzey et al. (1968) found *D. imbricata* to be a major predator of actinians along the rocky outer coast of Washington; yet, in the protected San Juan Islands, its diet was composed primarily of holothurians. At Waddah and Tatoosh Islands off Washington, they observed *D. imbricata* feeding on encrusting sponges, colonial tunicates, hydroids, and calcareous ectoprocts. Other localities indicate still additional diets. Feder (personal communication) observed leather stars with stomachs everted on eel grass, *Zostera marina*, in the intertidal regions of Prince William Sound, Alaska.

Off Pt. Loma, California we have observed *D. imbricata* feeding on *Strongylocentrotus purpuratus* (sea urchin), *Strongylocentrotus franciscanus* (sea urchin), *Astrometis sertulifera* (sea star), *Pisaster giganteus* (sea star), *Tethya aurantia* (sponge), *Leucilla nuttingi* (sponge), *Membranipora membranacea* (bryozoan), *Epiactis prolifera* (sea anemone), *Corynactis californica* (sea anemone), *Astrangia lajollaensis* (coral), *Muricea californica* (gorgonian), *Kelletia kelletii* (gastropod) egg capsules, unidentified sponges, holothurians, and detritus. *Strongylocentrotus purpuratus* made up 47% of the feeding observations; *L. nuttingi*, 13%; *A. sertulifera*, 4%; detritus, 27%; and all other items combined, 9%, out of a total of 437 feeding leather stars (Figure 1). Over a one-year period, 927 *D. imbricata* were examined for food items; however, some of these observations were repetitive in that the same leather star was reexamined on a different day of observation.

Feeding was accomplished by either ingesting the prey whole or by everting the stomach and

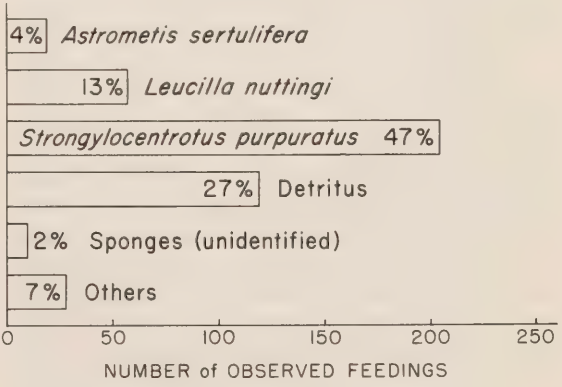

FIGURE 1.—Leather star feeding observations ($N = 437$) off Pt. Loma, California from November, 1969 through November, 1970.

digesting the prey outside of the mouth. Most of the feeding we observed was extraoral in that the leather star's stomach was partially everted out of the mouth (Figure 2). However, the distinction between the two types of asteroid digestion cannot always be determined, since "some species may digest prey partly inside and partly outside the mouth opening at the same time," (Feder and Christensen, 1966, p. 96). In contrast to our observations off Pt. Loma, Mauzey et al. (1968) found that *D. imbricata* usually ingested its prey whole. Again, digestion and method of feeding appears to be dependent on the size and form of the prey species. Often leather stars were observed with their stomachs extended into depressions or everted onto the substrata. In this situation we usually could not identify the food item; however, if the leather star's stomach was everted and there was no prey visible, we assumed that it was feeding on detritus. When feeding observations from the various regions are examined in total, the leather star appears to have a highly variable diet; however, when each location is considered separately the diet becomes much more specialized or restricted.

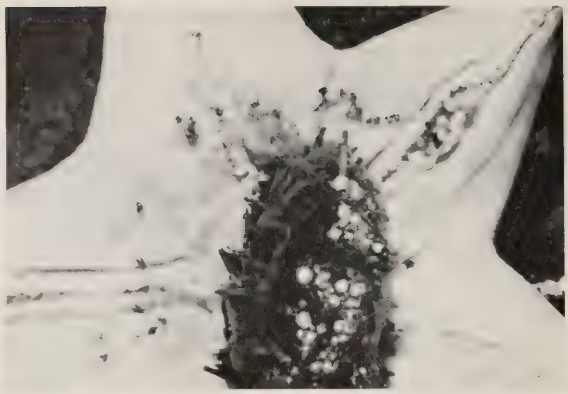

FIGURE 2.—*Dermasterias imbricata* feeding on a purple urchin 15 m underwater off Pt. Loma. Note the *S. purpuratus* pedicellariae attached to the leather star's epidermis.

PREDATION ON *Strongylocentrotus purpuratus*

Our data indicate that the leather star is a major predator of *S. purpuratus* off Pt. Loma. Of the 437 *D. imbricata* observed feeding, 204 or 47% were preying on *S. purpuratus* (Figure 1). However, this feeding behavior may be an areal phenomenon or even specific to Pt. Loma, since purple urchin predation by leather stars has not been reported from other regions along the Pacific Coast. Mauzey et al. (1968) did not find urchins included in the diets of *D. imbricata* off the coast of Washington, despite the presence of *S. purpuratus, S. franciscanus,* and *S. drobachiensis.* All three of these echinoid species appeared to be available to the *D. imbricata* that inhabited these subtidal areas (Dayton, personal communication). One explanation for the exclusion of urchins in the diets of leather stars off Washington might be the availability of alternate or "preferred" prey species. The sedentary or sessile invertebrates which Mauzey et al. (1968) found in the diets of *D. imbricata* off Washington did not appear to be important numerical constituents of the epibenthic community off the Pt. Loma study site. However, the sea urchin population had increased to a point where Leighton, Jones, and North (1966) suggested that perhaps an ecological imbalance had developed within these stands of giant kelp. Further, North and Pearse (1970) reported that an apparent population "explosion" of herbivorous sea urchins had occurred along the coast of Southern California.

In addition to the high percentage of leather stars observed eating purple urchins, we found that 51% of all *D. imbricata* examined off Pt. Loma had *S. purpuratus* globiferous pedicellariae attached to their epidermis (Figures 2 and 3). A laboratory experiment was performed to determine the maximum length of time that globiferous pedicellariae remain attached to the leather star following contact with a purple urchin. We found that following attachment, 3 to 4 days elapsed before the pedicellariae detached from the leather stars. A *D. imbricata* with purple urchin pedicellariae attached to it provided us with indirect evidence that the leather star had either eaten, or had contact with, one or more purple urchins within the last 3 to 4 days. In either case, the number of

FIGURE 3.—Globiferous pedicellariae from *S. purpuratus* attached to the arm of a leather star following contact between the two species in the laboratory.

contacts between the two species off Pt. Loma appears to be quite frequent.

Both species are conspicuous and abundant members of the benthic community within the study area. *Strongylocentrotus purpuratus* was found in densities between 0 and 100 individuals per m^2, with 30.2/m^2 as the mean value within the 16 randomly placed m^2 quadrats. Purple urchin density appeared to vary with the type of substratum. The greatest concentrations of purple urchins were found along or within the siltstone ledges.

We found *D. imbricata* in densities between 0 and 7 individuals per 100 m^2 in the 2,400 sq m of sea floor that was examined quantitatively. Leather stars were most abundant near siltstone ledges and rocky outcrops, where the highest concentrations of purple urchins were also found.

In most instances leather stars were observed feeding on purple urchins which were located in holes or depressions (Figure 4), under ledges, or in the holdfasts of giant kelp. Rarely was urchin predation observed on uniform substratum devoid of irregularities or discontinuities in the bottom. In the field we have observed *S. purpuratus* reacting to the presence of *D. imbricata*. When an approaching leather star disturbed an urchin tactually, it usually evoked a running or escape response. The *S. purpuratus* that inhabited substrata where avoidance maneuvers were possible usually escaped from pursuing leather stars. However, when purple urchins occupied depressions or irregularities along the sea floor, they became more vulnerable to asteroid entrapment and predation.

FIGURE 4.—Leather star feeding on a purple urchin. The sea star has pressed its oral surface into a depression to reach the prey.

In the laboratory most of the purple urchins that were preyed upon were captured on the sides of the water table at the water-air interface. Predation, in this case, appeared to be an artifact of the aquarium, since the two species do not experience this water-air barrier in the sublittoral zone. However, this interface was one of the few physical obstacles besides the corners of the water table that hampered the escape of the purple urchin, and thus allowed a pursuing leather star to capture it. In a similar observation, Mauzey et al. (1968) found that *S.*

purpuratus tended to move to the top of a tank and stop when pursued by *P. helianthoides* in the laboratory.

The 162 *D. imbricata* which were found feeding on whole purple urchins ranged in size (radius) from 79 mm to 166 mm, with 118 mm as the mean value. In comparison, a sample (N = 344) of the leather star population within the perimeter of the study area contained individuals from 50 mm to 202 mm and had a mean size value of 108 mm. The purple urchins that were preyed upon ranged from 12 mm to 52 mm in test diameter, with a mean value of 34 mm and a standard deviation of 8.5 mm. For comparative purposes we removed 494 *S. purpuratus* from 16 randomly selected m^2 quadrats. These urchins ranged from 7 mm to 60 mm in diameter and had a mean value of 39 mm and a standard deviation of 8.8 mm. Using these data we compared the mean of the *S. purpuratus* prey and the mean of the urchin population using a *t*-test. We found that at the 5% level there was a significant difference between the two means. It appeared as though the *D. imbricata* were feeding on a smaller size class of *S. purpuratus* than was available to them from the urchin population (Figure 5).

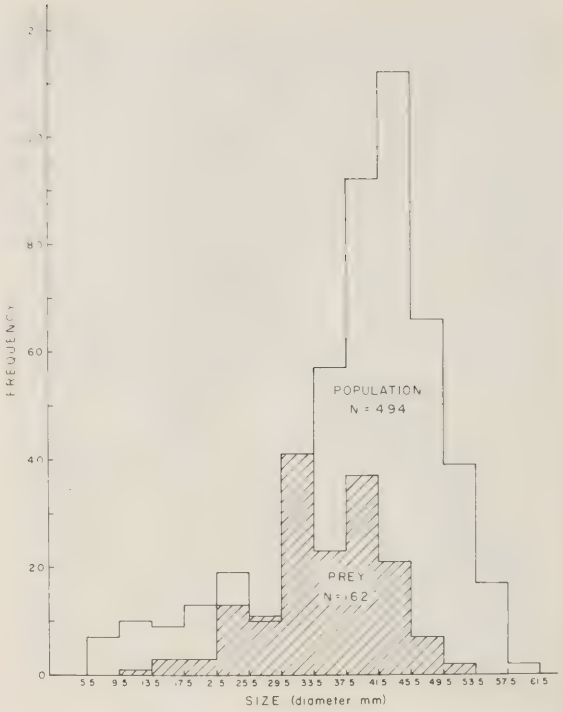

FIGURE 5.—A size frequency histogram comparing the 162 *S. purpuratus* prey with a sample (N = 494) from the urchin population within the Pt. Loma study area.

Landenberger (1968) found that in the laboratory large *Pisaster* spp. tended to eat large mussels. To determine if an optimal predator-prey size relationship existed between *D. imbricata* and *S. purpuratus*, the size of each predator and its prey was recorded as a point on a scatter diagram (Figure 6). A non-parametric corner test of association or independence was then applied to these data. We found that the two variables (predator size and prey size) were independent at the 95% level of significance. Therefore, no association between the size of a leather star predator and the size of a purple urchin prey is believed to exist. There was, however, an upper limit to prey size in that we observed no predation on purple urchins greater than 52 mm in test diameter.

FEEDING AND DIGESTION RATES

Most of the purple urchins we observed were killed and digested extraorally by leather stars following capture. However, purple urchins smaller than about 22 mm in test diameter were usually ingested whole. Kjerskog-Agersborg (1918) found that the sea star, *Pycnopodia helianthoides*, digested large prey extraorally, whereas smaller prey were regularly ingested whole.

Determining the feeding rate or number of purple urchins which can be eaten by a leather star over a given period of time was perhaps the most inconclusive aspect of the study. The experiment where leather stars and purple urchins were confined within a 4 m^2 area provided little information on feeding rates in nature. Although three urchins were eaten during the first seven days of observation, we observed no further predation after this initial period. We concluded that the enclosure interfered with the normal movements of the experimental animals, since the four leather stars were fre-

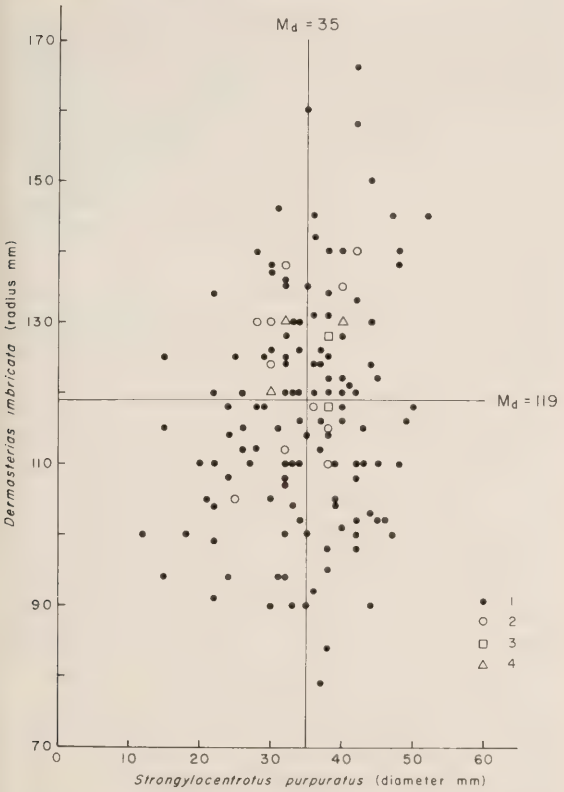

FIGURE 6.—Size of the leather star predator vs the size of the purple urchin prey. Open symbols indicate two or more identical data points.

quently observed crawling on the frame or the wire mesh of the cage.

Our tagging efforts in the field proved to be somewhat more valuable. The disc tags remained attached to the leather stars for at least eight months. During this period we were able to study the feeding behavior of tagged *D. imbricata* on an individual basis. The tagging procedure might have inhibited normal feeding behavior in *D. imbricata*; however, we observed leather stars actively feeding within three days after being marked. Out of 69 marked individuals, the maximum rate of urchin predation occurred with a 151-mm leather star. This individual was observed feeding on three purple urchins (32-36 mm) during seven consecutive days of underwater observations.

Laboratory feeding observations were carried out for 20 days. During this period every one of the seven *D. imbricata* in the water table preyed on at least one *S. purpuratus*. One leather star (140 mm) fed on three purple urchins (16-38 mm) during a five-day period. Sixteen of the 76 *S. purpuratus* present were eaten by the leather stars. The prey ranged from 15 mm to 42 mm in diameter.

From these observations it was learned that the digestion of a purple urchin's soft tissues usually took between 20 and 48 hours. However, on one occasion a 138-mm *D. imbricata* completely digested a 22-mm purple urchin in seven hours. Fisher (1928) reported that *P. helianthoides* digested the soft parts of *Strongylocentrotus* spp. in 24 to 36 hours. The digestion rate varied with the size of the leather star and the size of the prey, as well as the method of digestion. Large purple urchins ($\geqslant$22 mm), which were usually digested extraorally, were not digested as rapidly as smaller urchins. As an example, 19 hours were required for a 140-mm leather star to digest a 16-mm purple urchin, whereas 28 hours were required for this same leather star to digest a 38-mm purple urchin.

As pointed out in the section on methodology, it was usually necessary to lift up or turn the leather star over to determine whether or not it was feeding on an urchin. In the laboratory, when we disturbed a leather star that had captured or was in the process of digesting a purple urchin, it retracted its stomach, released hold of the urchin, and moved away from the prey. A similar disruption in feeding behavior was also noticed in the field. By marking the *D. imbricata* we had a method which we thought would allow us to study the feeding behavior of individual leather stars in nature. However, the tactile sensitivity that most members of this species displayed negated most of the benefit attained from individual recognition.

One physical factor in nature which appeared to influence predation on *S. purpuratus* by *D. imbricata* was water turbulence. The incidence of urchin predation decreased when a long-period swell generated a strong surge along the bottom off Pt. Loma. For example, on 9 January 1970, we recorded 48% of the *D. imbricata* ob-

served (N = 60) to be feeding on *S. purpuratus;* in contrast in this same area on 3 June 1970, only 13% of the leather stars observed ($N = 58$) were eating urchins. On the former day we noted that it was extremely calm underwater, while on the latter a very strong surge prevailed along the bottom at a depth of 15 m. We felt that there was a correlation between water movement and urchin predation by *D. imbricata,* although we had no quantitative measurement of this parameter. Feder (1956 and 1970) found that populations of *P. ochraceus* ate much less in relatively unprotected intertidal areas than in areas which provided the sea stars better protection from wave action.

SPECIES-SPECIFIC REACTIONS

Strongylocentrotus purpuratus reacted to the presence of *D. imbricata* by exhibiting defensive, as well as escape or avoidance, responses. No visible responses were exhibited by *S. purpuratus* which could be considered predator-induced until it was actually touched by a leather star. The podia or tube feet of the purple urchin appeared to be active sites for the reception of chemical and tactile stimuli (Figure 7). In regular urchins, such as *S. purpuratus,* the podia are symmetrically spaced and arranged in five double rows along the sea urchin's test. These podia are capable of extending nearly twice the length of the primary spines and function somewhat like the tentacles or antennae of other marine invertebrates. If viewed from the aboral surface, the area of sensory reception surrounding *S. purpuratus* can best be illustrated by drawing a circle around the urchin, with the locus of the points touching the tips of the fully extended podia.

In the laboratory sea urchin podia were touched with various biotic and abiotic objects to determine which ones elicited avoidance or defensive responses. When touched with human skin, a glass rod, or a "non-predatory" invertebrate, the podia in contact usually retracted and then were extended again. However, if the podia of a purple urchin touched a leather star, the urchin displayed definite signs of predator awareness: in the region of the tactile stimulus, the podia retracted rapidly, spines were depressed, and the poisonous globiferous pedicellariae gaped and became erect (Figure 8). In most instances the urchins moved in the opposite direction of the leather star stimulus.

In another experiment we tested the response of *S. purpuratus* to additional stimuli, using the gaping of the globiferous pedicellariae as an overt sign of predator recognition. The test animals were taken from two populations of *S. purpuratus.* One group was from the jetty in-

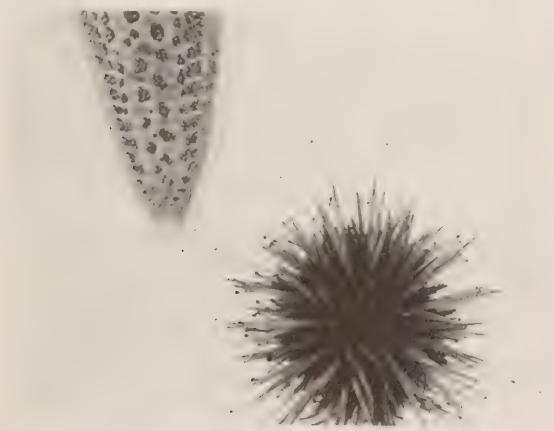

FIGURE 7.—*S. purpuratus* with extended podia just prior to initial contact with the arm of a leather star.

FIGURE 8.—The defensive behavior of *S. purpuratus* immediately after being touched by *D. imbricata.*

side Mission Bay, San Diego County (lat 32° 45'30" N; long 117°14'30" W), and the other was from the study site off Pt. Loma. Asteroid tube feet were selected as the biotic stimuli because of the known effectiveness of this tissue in eliciting avoidance reactions in other invertebrate species (Bullock, 1953). Coarse, washed sand grains were used as the abiotic control. Purple urchins were placed individually into glass bowls which contained seawater, and then an asteroid tube foot, or sand grain, was dropped onto the urchin's test. Each urchin was tested for a 2-min period using a different stimulus on each run. Fresh seawater was placed into the bowls prior to each test. The tube feet of *D. imbricata* elicited gaping and erection of purple urchin globiferous pedicellariae in 28 out of 30 test animals. These 28 individuals had an average reaction time of 8 sec, with a range between 2 and 20 sec. None of the *S. purpuratus* displayed gaped globiferous pedicellariae when either *Pisaster giganteus* tube feet or sand grains were presented to them.

Additional asteroids that were found in the sublittoral zone off Pt. Loma were also tested. The tube feet from *Astrometis sertulifera, Patiria miniata,* and *Pycnopodia helianthoides* evoked the pedicellariae response in *S. purpuratus;* however, no response was elicited when eight other asteroid species were tested (Table 1). It is interesting to note that the former three species were the only other sea stars, besides *D. imbricata,* that have been observed feeding on live *S. purpuratus* off Pt. Loma.

TABLE 1.—A list of sea stars found off Pt. Loma, California. All 12 species were individually used to test the globiferous pedicellariae response in *S. purpuratus.*

Species	Reaction
Astrometis sertulifera	+
Astropecten armatus	—
Dermasterias imbricata	+
Henricia leviuscula	—
Linckia columbiae	—
Mediaster aequalis	—
Patiria miniata	+
Pisaster brevispinus	—
Pisaster giganteus	—
Pisaster ochraceus	—
Orthasterias koehleri	—
Pycnopodia helianthoides	+

+ = pedicellariae response
— = no pedicellariae response

The erection and gaping of the globiferous pedicellariae initially occurred only on the area of the urchins' test which was directly stimulated by the sea star's tube foot. Jensen (1966) found that a single tube foot from the sea star, *Marthasterias glacialis,* activated the globiferous pedicellariae only in a restricted area on the test of the sea urchin, *Psammechinus miliaris,* whereas the sea star arm tip caused a response from all globiferous pedicellariae. In contrast, we found that the arm tip of *D. imbricata* activated the pedicellariae of *S. purpuratus* only in the region of the stimulus. The defensive response and recognition of predatory stimuli was so acute in *S. purpuratus* that an arm of a *P. giganteus* placed on one side of a purple urchin's test, and a *D. imbricata* arm positioned on the opposite side elicited a response from the globiferous pedicellariae only in the area of leather star contact.

Defensive use of globiferous pedicellariae by sea urchins when disturbed by predatory asteroids has been described by Prouho (1890), Jennings (1907), Jensen (1966), Mauzey et al. (1968), and Rosenthal and Chess (1970). Jensen (1966) reported that the poison contained in globiferous pedicellariae of *Psammechinus miliaris* was not strong enough to paralyze a *M. glacialis;* however, it did have an irritating effect on the sea star which caused it to retreat from the urchin. We found that in some laboratory situations, globiferous pedicellariae bites on the arms of *D. imbricata* caused localized withdrawal of gills or papulae, and a shortening or retraction of the affected arm. Despite this irritation, 90% of all the leather stars we found feeding on purple urchins had from one to over 300 sea urchin pedicellariae attached to their epidermis.

Certain groups of aquatic organisms have been observed to respond to chemical signals or alarm substances emitted by injured conspecifics (von Frisch, 1941; Pfeiffer, 1963; Snyder and Snyder, 1970). Recently, Snyder and Snyder (1970) found that the tropical sea urchin, *Diadema antillarum,* exhibited an alarm or escape response when stimulated with the juices of injured members of its own species. Laboratory and field

tests were conducted to determine if a similar alarm response existed in *S. purpuratus*. A purple urchin within a group of urchins was crushed underwater, and the reactions of neighboring conspecifics noted for 5 min. In both situations we observed no change in movement or alteration in behavior which could be considered alarm oriented following injury to a conspecific. In place of an alarm response we occasionally noted an entirely different reaction from *S. purpuratus* in the laboratory. If a leather star was disturbed while feeding on a purple urchin or moved away from an urchin test following predation, occasionally other *S. purpuratus* in the aquaria approached the conspecific and scavenged the remains.

DISCUSSION

The behavioral responses exhibited by *S. purpuratus* when it is disturbed by *D. imbricata* suggest a well-developed predator-prey relationship. In most instances purple urchins erected globiferous pedicellariae when touched by the four sea stars (*D. imbricata, P. helianthoides, A. sertulifera,* and *P. miniata*) which are known to prey upon them. In contrast, no evasive or defensive responses were noted in the same purple urchins when they were touched by eight additional asteroid species. It appears as though *S. purpuratus* either responds to sea stars that are biochemically similar, or through selection the urchin has acquired the ability to recognize particular asteroid species as potential predators.

The predator-prey association which exists between these two species off Pt. Loma, California may be a regional phenomenon, since the relationship has not been reported from other localities along the Pacific Coast. However, from the responses in both laboratory and field situations we believe that the occurrence is probably more widespread than indicated in the literature. The large number (47%) of *S. purpuratus* we found included in the overall diets of leather stars off Pt. Loma, as opposed to the total exclusion of this species in the diets of leather stars off Washington state as reported by Mauzey et al. (1968) is extremely puzzling to us. We can only speculate at this time on what could account for this variation in feeding behavior. Selection of potential prey by *D. imbricata* may be determined by the following conditions: (1) Prey density and availability, (2) search time or the time required by the sea star to find and capture suitable prey, (3) taste or gustatory preferences of the sea star, and (4) some form of associative learning by *D. imbricata.*

Strongylocentrotus purpuratus appeared to be available to *D. imbricata* on almost a continuous basis within the study area, since the population of purple urchins was estimated to have a mean density value of 30.2/m^2. Predator search and capture time also seems to be related to the density and distribution patterns of the prey, as well as to the avoidance tactics employed by these potential prey. Encounters between the two species on uniform substratum usually resulted in the escape of *S. purpuratus;* however, when the purple urchins occupied depressions, holes, or crevices along the sea floor, they became more vulnerable to asteroid predation. In response to asteroid predation *S. purpuratus* has apparently evolved countermeasures such as evasive movement, and defensive utilization of spines and poisonous globiferous pedicellariae. The large number (90%) of feeding leather stars with purple urchin pedicellariae attached to their epidermis might lead one to suspect that these appendages are ineffective as a defensive mechanism. The pedicellariae, however, appear to act as an irritant that in certain situations halts the pursuit of a leather star and thus allows the urchin to escape. Marler and Hamilton (1966, p. 142) stated that "there is evidently a subtle and dynamic balance between these different evasive characteristics of the prey species on the one hand and the abilities of the predators to overcome them on the other". The taste or gustatory preferences of individual *D. imbricata* as compared to a leather star population has not been explored.

From our observations off Pt. Loma we would expect that at least a few purple urchins would show up in the diets of *D. imbricata* off Washington, even if other species were "preferred" above *S. purpuratus.* Possibly before leather stars prey on live urchins there is a learning

process involved before the sea star recognizes or associates specific stimuli with food. Tinbergen (1960) proposed that learning was involved in the feeding behavior of insect-eating birds, and that initial non-acceptance of specific insects by these birds was due to an unfamiliarity with these forms as prey. He further related initiation of feeding on a new food item with chance experience and prey density. Tinbergen (1960) suggested that the predator acquires a "specific search image" for the prey after being sufficiently impressed with it from frequent chance encounters. Holling (1958 and 1965) studied predation on the cocooned pupae of sawflies by shrews and mice, and suggested that associative learning was an important component in the feeding behavior of these small mammals.

Unfortunately, associative learning has been studied in only a relatively small number of lower animal (invertebrate) groups. Evans (1968) discussed this form of learning in cephalopods, insects, annelids, and flatworms. There is some evidence to suggest that associative learning exists in echinoderms. Landenberger (1966) found that the sea star *P. giganteus* learned to associate a light stimulus with food. The association apparently disappeared when the response to the light stimulus was no longer rewarded with food. If associative learning, with food as a reinforcement or reward, is a component in the feeding behavior of *D. imbricata*, then it might account for the presence of purple urchins in the diets of leather stars off Pt. Loma. This area contained a large number of highly accessible *S. purpuratus*, and yet at the same time appeared to be practically devoid of many of the sessile or sedentary invertebrates that these sea stars are reported to feed on. *Dermasterias imbricata* probably responds to a small class of chemical and/or tactile stimuli; however, only through associative learning and experience can it exploit an evasive prey species such as *S. purpuratus*. The leather star may not acquire the experience necessary to capture live *S. purpuratus* in other subtidal areas that contain alternate prey in greater abundance, since these forms are more accessible and possibly can account for the total nutrient requirements of *D. imbricata*.

ACKNOWLEDGMENTS

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COMPARISON OF FOREGUT CONTENTS OF *Sergestes similis* OBTAINED FROM NET COLLECTIONS AND ALBACORE STOMACHS

David C. Judkins and Abraham Fleminger[1]

ABSTRACT

Sergestes similis, an oceanic shrimp, was taken at a number of locations in the eastern North Pacific, principally in the California Current region. The contents of foreguts from shrimp caught by net during the day and night and those of shrimp eaten by free-swimming fish were compared. In all three categories of foreguts the predominant prey were adult specimens of the larger, common calanoid copepods which typically inhabit the upper 200 to 300 m in the California Current region. However, because the diversity of calanoid species and the numbers of fish scales, calanoids, and euphausiids were appreciably greater in the foreguts of net-caught *S. similis* than in fish-caught samples, it appears likely that *S. similis* feeds in collecting nets under tow.

Sergestes similis Hansen is an abundant pelagic shrimp endemic to North Pacific waters of boreal-temperate influence (Pearcy and Forss, 1969; Judkins, unpublished data). Examination of its stomach contents indicates it is predaceous and feeds primarily on copepods and euphausiids (Renfro and Pearcy, 1966).

There is an expanding body of evidence that, in the freshwater environment, predation by planktivores is size selective and determines, in part, the composition of zooplankton communities (Brooks and Dodson, 1965; Brooks, 1968; Dodson, 1970; Hall, Cooper, and Werner, 1970). Size-selective feeding by an abundant oceanic carnivore such as *S. similis* may play an important role in limiting the abundance of an array of prey species within a size range and, hence, in determining the composition of the zooplankton community within its habitat. The first step in determining the impact of *S. similis* as a predator in the community is to identify and to enumerate the prey species it utilizes.

In this report we identify and enumerate the foregut contents of *S. similis* from net tows and albacore stomachs taken at a number of localities in the eastern North Pacific. To determine if the results were affected by feeding in the net or by diurnal changes in feeding intensity and diet, comparisons were made between three categories of specimens: day-net samples, night-net samples, and fish-stomach samples.

MATERIALS AND METHODS

About two thirds of the 270 foreguts with contents examined in this study were obtained from *S. similis* collected by nets, principally Isaacs-Kidd midwater trawls, over several seasons (Table 1). The remaining one third were obtained from troll-caught albacore taken in July-August 1968 (Laurs and Nishimoto, personal communication). With the exception of one net tow taken in the Gulf of California all of the collections were made in the northeast Pacific Ocean between lat 31° and 53° N (Table 1).

Carapace lengths (measured from the tip of the rostrum to the dorsal mid-point of the posterior margin) of the net-caught shrimp ranged from 6.5 to 17.0 mm, with a median of 11.3 mm. Carapace lengths of fish-caught shrimp ranged from 6.3 to 12.5 mm, with a median of 8.3 mm. Because many fish-caught shrimps were partially digested, it was necessary to estimate their carapace lengths from the lengths of their foreguts (Judkins, unpublished data).

The foreguts were removed intact from the specimens with fine forceps and placed on glass

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TABLE 1.—Material examined.

	Collection number	Gear	Date	Position		Time (GCT)	Depth	Sample size
				Latitude N	Longitude W		m	
Night net	Northern Anchovy 10	KMT	1 Aug 1951	40° 08'	150° 30'	2130-2200	175	10
	CalCOFI 6004-M 60.80	KMT	26-27 Mar 1960	32° 27'	122° 37'	2024-0006	1,673	9
	60.90	KMT	28 Mar 1960	36° 04'	126° 46'	0012-0147	298	10
	80.86	KMT	1 Mar 1960	34° 19'	120° 46'	1900-2106	296	10
	80.90	KMT	7 Mar 1960	34° 07'	121° 38'	2100-2206	300	10
	80.40	KMT	17 Apr 1960	31° 21'	117° 27'	2029-2414	298	3
	Jane Meyer 10	KMT	3 Aug 1964	49° 01'	155° 00'	2027-2411	245	10
	24-Shallow	BMOC[2]	28 Aug 1964	47° 28'	155° 30'	2216-2236	100-75	4
	Reber II Birch 4	Tucker[3]	14 Feb 1966	48° 12'	148° 07'	0602-0656	450	10
	KM 66-M1	KMT	30 Jan 1966	29°	117°	2245-0307	1,000	10
	Total							86
Day net	Northern Anchovy 10	KMT	1 Aug 1951	50° 28'	146° 06'	1945-1655	450	6
	CalCOFI 6004-M 60.70	KMT	27 Mar 1960	30° 07'	124° 28'	0613-0750	298	4
	60.100	KMT	28 Mar 1960	36° 17'	126° 01'	0809-1006	1,863	3
	80.70	KMT	7 Mar 1960	33° 54'	121° 50'	0948-1424	1,863	5
	Jane Meyer 24-Deep	BMOC	28 Aug 1964	46° 15'	155° 00'	1640-1809	300-400	10
	Reber II Birch 3	Tucker[3]	14 Feb 1966	47° 54'	148° 29'	1519-1553	--	10
	SIO 67-101	KMT	9 June 1967	35° 16'	122° 16'	0627-1584	2,200	10
	SIO 67-102	KMT	10 June 1967	36° 19'	123° 06'	0705-1402	2,200	9
	SIO 67-10	KMT	14 June 1967	37° 20'	123° 42'	0558-1150	2,200	8
	Total							65
Twilight net	CalCOFI 6004-M 80.60	KMT	16 Apr 1960	32° 28'	120° 06'	0450-0620	148	10
	SIO 66-6	KMT	21-22 May 1966	40° 35'	126° 50'	2000-0040	1,125	11
	SIO 67-47	KMT	20 Apr 1967	31° 36'	117° 54'	1508-1900	4,000	10
	Total							31
Fish stomachs	AD 66 Stomach 1-6	Trawl	16 July 1966	~ 56°	~ 156°	1815		11
	208		17 June 1966	~ 54°	~ 164°	--		2
	241		16 June 1966	~ 56°	~ 166°	1210		24
	248		16 June 1966	~ 56°	~ 166°	1800		10
	92		18 June 1966	~ 58°	~ 167°	--		17
	79		20 June 1966	~ 42°	~ 127°	--		2
	140		21 June 1966	~ 44°	~ 127°	--		4
	58		2 Aug. 1966	~ 44°	~ 135°	--		5
	9		2 Aug. 1966	~ 45°	~ 134°	0955		15
	204		8 Aug. 1966	~ 56°	~ 165°	0615		10
	Total							100

[1] Isaacs and Kidd, 1960.
[2] McGowan and Brown, 1966.
[3] Tucker, 1951.

microscope slides where their contents were emptied into 100% glycerol. All observations were made with aid of a stereomicroscope or a compound microscope at various magnifications as needed from 16× to 1000×.

The contents were examined to identify and enumerate all particles. Several drops of lactic acid tinted with chlorozol Black E were added to the glycerol to facilitate identification of the components. Lactic acid aids in clearing the preparation. The tint stains the components and is especially useful for arthropod cuticle. The identity of crustacean prey was often established from the morphology of mandibles, genital segments, fifth legs, or other diagnostic features.

In Table 1, collection numbers grouped by the designation "night-net" represent a set of 10 samples varying in number from 3 to 10 shrimp each and collected by nets that were towed exclusively between sunset and sunrise. Collection

numbers designated "day-net" comprise a set of nine samples of from 3 to 10 shrimp each and collected by nets that were towed exclusively between sunrise and sunset. "Twilight-net" collection numbers represent three samples collected by nets which were actually towed at sunset or sunrise. Collection numbers designated "fish stomachs" represent 10 samples of 2 to 24 shrimp taken from stomachs of albacore. The albacore were taken during daylight hours by trolling lines; exact times of capture were not available for five of the specimens.

Included in statistical analyses were all classes of food occurring in 10% or more of any of the sets of night-net, day-net, and fish samples. Calanoid genera occurring in 10% or more of any of the sets of samples were considered separately. The small number of twilight-net samples was not included in statistical comparisons of the sampling categories, but the details of this set are given in Table 2. Overall means (no. prey foregut) and frequencies (%) were calculated for the three sets of samples that were compared. In addition, means were calculated for each night-net, day-net, and fish sample. The Mann-Whitney *U*-Test, a test designed to estimate the significance of differences in median values of two samples was used to compare median sample means between day- and night-net samples and between combined day- and night-net samples and fish samples.

RESULTS

Ingested items included euphausiids, ostracods, amphipods, chaetognaths, and fish scales, but the principal identifiable components in all sampling categories were adult calanoid copepods (Table 2). The composition of foregut contents from different geographical regions (North Pacific Subarctic, North Pacific Drift, and the California Current) were very similar and hence were not considered separately. The diversity of calanoids was much greater in all categories of net samples than in fish samples: 42 species were identified in net samples, but only 7 were found in fish samples.

Foregut contents varied widely in the extent of maceration by digestion and mastication.

TABLE 2.—List of organisms and their frequency of occurrence in the foreguts of *Sergestes similis*

	Night-net	Day-net	Twilight-net	Fish
Copepoda				
[illegible]	4	--	--	--
[illegible]	1	3	--	--
[illegible]		3	--	--
[illegible]		1	--	--
[illegible]	30	71	3	--
[illegible]	78	73	3	--
[illegible]	--	--	3	10
[illegible]	--	--	1	1
[illegible]	--	1	--	--
[illegible]		--	--	--
[illegible]	5	3	--	--
[illegible]	3	1	--	--
[illegible]		--	--	--
[illegible]		--	--	1
[illegible]	15	13	3	--
[illegible]	4	3	--	--
[illegible]		1	--	--
[illegible]	13	7	4	1
[illegible]	1	2	1	--
[illegible]	--	--	--	--
[illegible]			--	--
[illegible]	2	1	--	--
[illegible]	1	1	--	--
[illegible]	1	--	1	--
[illegible]	1	1	--	--
[illegible]	--	1	--	--
[illegible]	--	--	1	--
[illegible]	15	18	5	20
[illegible]	30	11	3	2
[illegible]	3	1	2	1
[illegible]		1	--	--
[illegible]		--	--	--
[illegible]	1	--	--	--
[illegible]	2	--	--	--
[illegible]	1	1	2	1
[illegible]	1	--	--	--
[illegible]	1	--	--	--
[illegible]	1	1	--	--
[illegible]	3	1	1	--
[illegible]	1	--	--	--
[illegible]	--	4	--	--
[illegible]	--	1	--	--
[illegible]	1	1	--	--
[illegible]	--	--	1	--
[illegible]	--	1	--	--
[illegible]	--	--	--	--
[illegible]	3	1	--	--
[illegible]	1	--	--	--
[illegible]	1	3	1	--
[illegible]	1	1	--	--
[illegible]	1	3	1	--
[illegible]	1	1	--	--
[illegible]		13	--	--
[illegible]	--	--	--	1
[illegible]	1	--	1	1
[illegible]	4	24	3	11
[illegible]	--	--	1	--
Euphausiacea				
[illegible]	13		3	3
unidentified	13	13	3	3
Ostracoda				
[illegible]		3		1
unidentified	1	--	1	5
Amphipoda				
unidentified	5	7	--	2
Chaetognatha				
unidentified	13	1	--	2
Fish scales	1	13	3	--
Fish eggs	1	--	--	--
Foraminifera unidentified	--	3	--	--
Radiolaria unidentified	--	1	--	1
Mollusca veliger	1	--	1	--
Cumacea unidentified	1	--	--	--
Cirripedia cypris	--	--	--	1
unidentified debris	20	20	10	42
Total number foregut with contents	80	85	31	88

Specimens in the same sample frequently varied from one another, and the degree of decomposition in each specimen usually was not uniform. Lightly digested prey were largely intact, and their internal organs still visible. Moderately digested prey contained obviously macerated tissue and were often incompletely fragmented. Prey in an advanced state were highly fragmented, and soft tissues were absent. Digestion of foregut contents tended to be less advanced in night-net than in day-net samples. However, most foreguts in both categories contained material in an advanced state of digestion.

Five groups of ingested material, calanoids, euphausiids, chaetognaths, fish scales, and unidentifiable matter, occurred in 10% or more of at least one of the three sampling categories (Figure 1). Unidentifiable material consisted primarily of crustacean fragments and matted aggregations of fibrous and granular debris. Of identifiable groups, calanoids were usually most abundant in all three categories (Table 3). The four identifiable groups of prey organisms appeared in higher numbers in net samples than in fish samples, differences between the median values, with the exception of chaetognaths, being significant at $P \leqslant 0.05$.

Frequencies, overall means, and median sample means of calanoids and euphausiids in day-net samples were less than were those in night-net samples. However, differences between the day and night median values of the four identifiable groups were not significant ($P > 0.50$). Twilight-net samples do not appear to differ appreciably from day- and night-net samples.

Calanoid genera occurring in more than 10% of the three categories (Figure 2) were *Metridia* (principally *pacifica*), *Calanus* (principally *pacificus*), *Pleuromamma* (principally *borealis*), *Rhincalanus* (all *nasutus*), *Euchaeta*, *Eucalanus* (principally *bungii*), *Scolecithricella*, and *Candacia* (principally *bipinnata*). These genera have been found typically in the uppermost 200 to 300 m of the California Current region (Fleminger, unpublished data).

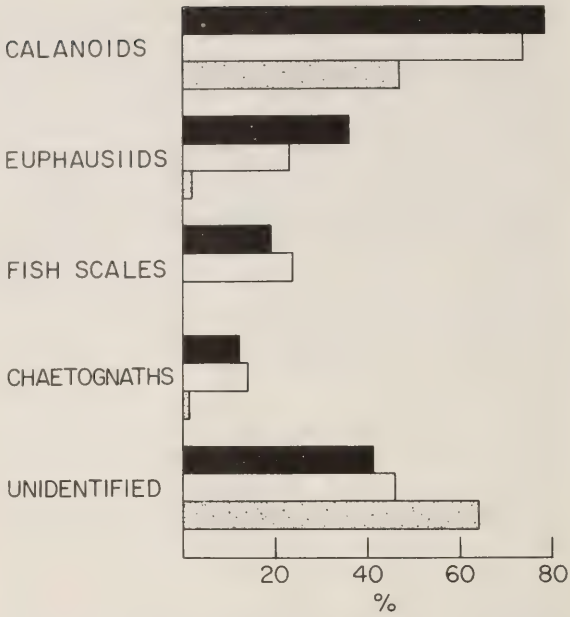

FIGURE 1.—Frequencies of ingested items occurring in 10% or more of night-net (black), day-net (open) and fish (strippled) samples.

The overall mean number of *Calanus* in day- and night-set samples are notably different (Table 4). In night-net samples *Calanus* ranked with *Metridia*, the two dominating the list of

TABLE 3.—Median of sample means and overall mean of number of prey per foregut.

Prey	Night-net			Day-net			Fish		
	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean
Calanoids	2.40	0-12.50	4.23	2.25	0.67-5.70	2.68	0.63	0-3.20	0.96
Euphausiids	.33	0- 2.90	.66	.10	0-1.50	.32	0	0- .12	.02
Fish scales	.10	0- 1.00	.31	.23	0-3.00	.37	0		0
Chaetognaths	.20	0- .30	.15	.16	0- .33	.14	0	0- .50	.02
Number samples	10			9			10		
Total number foreguts	86			65			88		

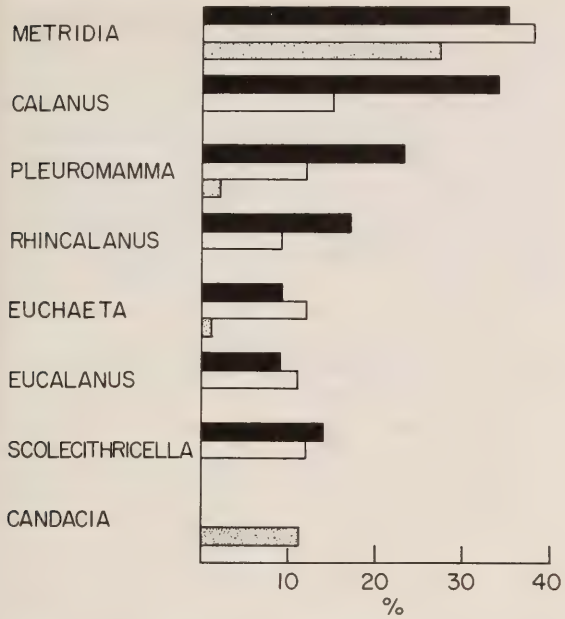

FIGURE 2.—Frequencies of calanoid genera occurring in 10% or more of night-net (black), day-net (open), and fish (strippled) samples.

calanoid prey. In day-net samples *Calanus* numbers are considerably below those of *Metridia* which remained high. However, the difference between the median sample means of *Calanus* in day- and night-net samples is not significant ($P > 0.20$). This is also true of the other seven genera.

Metridia was numerically dominant in fish samples, although it occurred in lower numbers than in net samples. Differences between the median sample means of *Metridia* in net and fish samples, however, are not significant ($P > 0.40$). Differences between net-and-fish-caught *S. similis* in the median values of *Eucalanus, Euchaeta,* and *Rhincalanus* are significant at P values falling between 0.10 and 0.20. Differences among the remaining calanoid genera are significant at P values between 0.02 and 0.10.

DISCUSSION

Metridia pacifica, Calanus pacificus, Pleuromamma abdominalis, Rhincalanus nasutus, Eucalanus bungii californicus, and *Candacia bipinnata* are among the 24 most abundant and frequently occurring of 176 calanoid species found in zooplankton samples collected on CalCOFI Cruises 5804, 5807, 5810, and 5901 (Fleminger, 1967). Significantly, these are also the principal species of six of the eight genera most frequently occurring in the foreguts examined in the present study. Adults of these species exceed 3 mm in length. It appears, then, that the principal prey of *S. similis* are the more abundant, relatively large, adult copepods inhabiting the uppermost 200 to 300 m in the California Current region.

Additional items found in both net and fish samples are euphausiids, chaetognaths, ostracods, amphipods, and radiolarians. Of these,

TABLE 4.—Median of sample means and overall mean in calanoid genera occurring in more than 10% of foreguts. [Means expressed as number of prey per foregut.]

Prey	Night-net			Day-net			Fish		
	Median	Range	Mean	Median	Range	Mean	Median	Range	Mean
Metridia	0.30	0-4.10	0.95	0.56	0-1.60	0.78	0.36	0-2.90	0.69
Calanus	.40	0-5.90	1.16	0	0- .80	.17	0		0
Pleuromamma	.30	0-1.10	.36	.10	0- .80	.15	0	0- .09	.02
Rhincalanus	.20	0-2.00	.35	0	0- .30	.09	0		0
Euchaeta	.10	0- .20	.10	0	0- .40	.14	0	0- .06	.01
Eucalanus	0	0- .30	.10	0	0- .50	.11	0		0
Scolecithricella	.10	0- .40	.13	.10	0- .30	.12	0		0
Candacia	0		0	0		0	.10	0- .50	.11
Number samples	10			10			10		
Total number foreguts	86			65			88		

only euphausiids were reported in a previous study on the diet of *S. similis* (Renfro and Pearcy, 1966).

A large percentage of shrimp of all sampling categories contained mixtures of granular and fibrous debris. The unidentifiable state of this material may not be entirely the result of digestive processes, but of the decomposed nature of the material at the time of its ingestion. *Sergestes similis*, like *S. lucens* (Omori, 1969), may scavenge decomposing dead material in addition to taking living prey. Another possibility is that this material represents the remains of prey stomach contents, e.g., those of euphausiids.

There is a tendency for day-net overall means to be less than those of night-net samples (Table 3). This and the trend toward less advanced digestion in night-net samples suggest more intense feeding activity at night, as was reported for *S. lucens* (Omori, 1969). The lesser average number of calanoids per foregut in day-net samples may be attributed primarily to the notably fewer *Calanus* in that category (Table 4).

Although the median values are not statistically different, day and night differences in overall mean numbers of the two calanoid species most frequently occurring in net samples, *Metridia pacifica* and *Calanus pacificus*, are notable in that they agree with differences in the vertical distributions of these two species. In the California Current region south of lat 33° N, *Calanus pacificus* usually concentrates in and near the thermocline during the day and disperses throughout the mixed layer at night. *M. pacifica*, on the other hand, occurs in the vicinity of the thermocline at night and disperses downward during the day (Fleminger, unpublished data). Studies have shown *S. similis* to be concentrated between the surface and 200 m at night and between 250 and 500 m during the day (Barham, 1957; Pearcy and Forss, 1966). The diurnal vertical range of *M. pacifica*, then, seems to correspond more closely with that of *S. similis* than does the diurnal range of *C. pacificus*. *Sergestes similis* probably has access to quantities of *M. pacifica* during both day and night. Most likely, *S. similis* encounters and feeds upon concentrations of *C. pacificus* primarily at night after the sergestid has ascended to shallower depths. However, without knowledge of digestive rates, these considerations are speculative.

The large numbers of fish scales in net samples and their complete absence in fish-stomach samples strongly suggest that feeding in the net has occurred. Although the source of these scales cannot be ascertained, it seems probable that they are the highly deciduous scales of lanternfish captured in the net with the shrimp. The significantly greater numbers of euphausiids and chaetognaths and the higher diversity of calanoids in net samples may also be indicative of feeding after capture. Many preserved net-caught *S. similis* have been observed by one of us (Judkins) to have fish scales, chaetognaths, and small crustaceans packed into their mouthparts and sometimes gripped in their mandibles.

Special conditions under which fish-caught shrimp might have been feeding before capture (related perhaps to time or depth) may also have contributed to the observed disparities between net and fish samples. Albacore are thought to feed primarily during daylight hours and probably most intensively in the early morning and early evening (Iversen, 1962). Time of capture by trolling of the albacore that we examined is available for only about half of the specimens. Of these about half were taken in morning daylight hours and the remainder were from the late afternoon and early evening. If all of the fish-caught shrimp were captured during the day, the relatively small quantities of identifiable components might reflect less intensive feeding by the shrimp at the time they were ingested by the albacore.

The generally smaller size of fish-caught specimens is probably not a factor; small net-caught shrimp (carapace length less than 10 mm) contained numbers of fish scales, euphausiids, and chaetognaths proportionally as high as larger net-caught individuals. Differences amongst sergestid specimens in the length of time spent in an albacore stomach also appear to be a negligible factor. Foregut contents of nearly intact fish-caught shrimp do not differ appreciably from those of extensively decomposed shrimp.

In general, the various samples of foreguts from adult *S. similis* that were analyzed provide

vide a coherent pattern of prey organisms consisting principally of the larger, commoner species of calanoid copepods inhabiting the uppermost 200 to 300 m of the California Current region. However, it is likely that feeding by *S. similis* in the net while it is being towed may explain the greater number and diversity of prey items in net-caught shrimp.

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NOTE

LONGEVITY AND GROWTH OF TAGGED KING CRABS IN THE EASTERN BERING SEA

During the period 1957 through 1959, the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) released 32,328 tagged king crabs, *Paralithodes camtschatica,* in the eastern Bering Sea. Since then several thousands have been recovered, 23 of which exceed previously reported maximum ages for this species (Table 1). These crabs were originally captured by Bureau research vessels, marked with serially numbered plastic spaghetti tags inserted through the isthmal muscle (method described in Alaska Fisheries Board and Alaska Department of Fisheries, 1955: 34-43), and released immediately. Crabs were recaptured by the crab tangle net fisheries of Japan and the Soviet Union, and recapture data were provided by the two nations as part of annual exchanges of scientific information called for by bilateral fishing agreements with the United States.

We estimated the ages of the crabs at release from size and age data for young king crabs published by Weber (1967). Weber found that both male and female king crabs in the eastern Bering Sea mature at about 95 mm carapace length; that males reach this size in 5 years and females in 5½ years (assuming a hatching date of late April to early May); and that immature crabs longer than 60 mm increased about 16 mm per molt. Growth curves for both sexes were similar up to the fourth year of life (length of 80 mm), but after the females become mature they grow slower. The males, however, continue to grow about 16 mm per molt throughout the rest of their lives (Weber and Miyahara, 1962; Hoopes and Greenough, 1970).

Total age was estimated for all four males, and length data are available for three of the four (Table 1). One male released in 1957 was recaptured in 1968, having been at liberty for 11 years. This crab was estimated to have been 6 years old at time of release, and if this estimate is correct, it was 17 years old at time of recapture. If the average growth per molt was 16 mm, this crab molted three or four times during the 11 years between release and recovery, and the other two crabs for which growth data are available molted only once or twice in 9 years. This molting frequency is much lower than that reported by Weber and Miyahara (1962), but we have no explanation for the reduced rate of molting in the two crabs. Before this study, the oldest known-age king crab reported in the literature was a male that was tagged near Kodiak Island and recaptured 20 miles from the release location 6 years and 4 months later (Powell, 1965). Powell estimated that this male was 7 years old when tagged and 13 years old when recaptured.

TABLE 1.—Carapace lengths and estimated ages of 4 male and 19 female king crabs tagged in the eastern Bering Sea by the National Marine Fisheries Service in 1957, 1958, and 1959 and recovered 1966, 1968, and 1969.

Sex and tag no.	Release date	Recovery date	Carapace length at—		Estimated age at—	
			Release	Recovery	Release	Recovery
Males			*mm*	*mm*	*years*	*years*
B5178	9/9/57	9/16/68	108	170	6	17
B7013	4/29/58	5/18/66	124	[1]	7	15
B7364	5/2/58	3/30/68	109	132	6	15
C8909	5/14/59	9/25/68	108	133	6	15
Females						
B7535	5/3/58	5/21/68	97	138	5	15
B7560	5/3/58	6/26/68	94	152	5	15
B7567	5/3/58	6/8/69	99	149	5	16
B7906	5/4/58	5/10/66	109	[1]	6	14
B8008	5/4/58	4/30/68	110	155	6	15
B8015	5/4/58	5/18/66	108	[1]	6	14
B8552	5/11/58	3/28/69	108	149	6	16
B9150	5/26/58	5/8/69	90	138	5	15
C2111	6/17/58	5/8/69	130	162	[illegible]	18
C2508	6/17/58	4/30/68	99	140	5	14
C2561	6/17/58	6/21/68	114	157	7	17
C2785	6/17/58	5/9/68	77	136	4	13
C2804	6/17/58	5/20/68	108	150	6	15
C3871	6/27/58	5/5/68	97	162	5	14
C3969	6/27/58	5/19/68	94	147	5	14
C4106	6/27/58	6/14/68	107	137	6	15
C4423	6/28/58	3/29/68	104	141	6	15
C4837	6/29/58	9/1/69	102	136	5	16
C5961	7/5/58	5/17/68	91	120	5	14

[1] Not available.

Length and age data are available for 17 of the 19 females (Table 1). One attained an estimated age of 18 years, having been at liberty for 10 years after being tagged. If these 17 females molted once each year, their growth per molt ranged from 3.1 to 7.2 mm (length); the average increment was 4.7 mm. This average value is similar to other reported annual growth increments for female king crabs in Alaska waters—4.4 mm (Powell, 1967), 3.9 mm (Gray, 1963), 5.0 mm (Bright, Durham, and Knudsen, 1960), and 4.0 mm (Sakuda, 1959).

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JAPANESE DISTANT-WATER FISHERIES: A REVIEW[1]

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ABSTRACT

Most of the industrialized fisheries of Japan have developed under a licensing system controlled by the central government. Limitations on entry and the allocation of resources based on a variety of social and economic considerations have resulted in the development of an extremely diversified industry.

The postwar expansion of distant-water fisheries greatly accelerated the exploitation of resources in the North Pacific, as well as in many other areas of the world, and has caused numerous international conflicts. In addition to regional conventions for high seas fisheries, various bilateral agreements have been negotiated to cope with problems arising from jurisdictional claims by coastal states. While supporting narrow limits of national jurisdiction and the concept of free access to high seas fishing, Japan has accepted different forms of allocation as a means to accommodate the conflicting interests of the nations involved. Her domestic institutions and organization of the industry have helped the government make pragmatic arrangements with other nations. Whether or not a general agreement on fishery issues can be reached at the new Law of the Sea Conference, Japan will face more and harder international negotiations in view of the general trend of coastal states claiming broader zones of national jurisdiction.

Each of the main sectors of the Japanese fishing industry, including inshore fisheries, offshore fisheries, distant-water fisheries, and aquaculture, now operates under severe constraints. Although the total catch of distant-water fisheries is still increasing due largely to intensified pollack fishing in the Pacific, long-term prospects for further expansion do not appear bright. Little progress has been made in the utilization of abundant resources of unconventional species. Thus, the rapid growth of domestic fishery production is unlikely to continue. Increased joint ventures and other business arrangements in foreign countries may provide a partial solution. Import decontrol for fishery products would contribute substantially to meeting immediate problems of supply shortage.

This paper was originally drafted to provide, as part of the NORFISH study under the Washington Sea Grant Program which is supported by the National Oceanic and Atmospheric Administration, some background information on the development and the present status of the Japanese high seas fisheries, particularly those which have bearing on various international arrangements in the North Pacific. Since, however, discussions on the future regimes of the sea have been carried out with increasing intensity, the emphasis of the paper has shifted somewhat from descriptive information to a more analytical study of the international fishery problems faced by the Japanese government and industry, as well as the courses of action they are likely to take in response to future changes in international regulatory regimes. The importance of the topic in considering future international arrangements for fisheries is obvious, for the Japanese and Soviet distant-water fisheries have been among the major sources of international conflicts over fishery matters in various parts of the world. Although emphasis is on the North Pacific, developments in the rest of the world are also covered to the extent that they have bearing upon the situation in the North Pacific.

The present paper is not a comprehensive study of the Japanese fishing industry to examine closely all sectors of the industry, including inshore, coastal, and distant-water fisheries, as well as processing and marketing

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aspects. It emphasizes those fisheries the development of which have had substantial effects on international regulation of fisheries, except for such passing references to other elements of the industry as considered relevant.[3]

One of the serious problems about writing an English paper concerning Japanese fisheries is that fishery institutions in Japan are extremely complex and difficult to understand. It is almost impossible for foreigners to fully comprehend institutional aspects of the Japanese fishing industry without having been in the country for some time. English literature in this area is meager. Yet, domestic institutions for fisheries have had such tremendous effects on development of all Japanese fisheries, including those in distant waters, that it is often irrelevant to discuss their problems without having some understanding of the institutional framework in which they operate. To obtain some general information on this aspect, the readers of this paper are referred to four English papers: Oka, Watanabe, and Hasegawa (1962), Kasahara (1964), Comitini (1967), and Herrington (1971).

All high seas fisheries discussed in this paper are rigidly regulated by what is called "the licensing system." The system controls the activities of each fishery through restrictions on the total number of licenses to be issued, size of vessels to be used, area of fishing, method of fishing, and often species to be taken. Although the actual regulations under this system differ from fishery to fishery, a common, and most important, feature is direct control on the number and types of vessels to be used for a particular fishery. The justifications used by the government for imposing the limited entry system on offshore fisheries has varied. Among apparent objectives are: protection of inshore fisheries against offshore fishing, reduction of competition and prevention of disputes between different groups of offshore fishermen, stabilization of fishing conditions, maintenance of profitability, conservation of resources, prevention of international disputes, and others. Degree of success in achieving these objectives has also differed from case to case, but there is no question that the system has served as a powerful and convenient means to control each fishery and introduce such changes as considered desirable by the Japanese fishery administration.[4]

Practically all offshore and distant-water fisheries discussed in this paper are regulated by the central government. While legal authority is vested in the Minister of Agriculture and Forestry, the Fishery Agency (Suisancho), which is subordinate to the Ministry of Agriculture and Forestry, has in fact full power to control all major fisheries. There still exist a large number of small fisheries regulated by the provincial authorities, but they have practically no international implications, except those operating off the southernmost part of the Kurile chain and in Korean Straits. Chapter 3 of the Fishery Law, as amended in 1963, provides that anyone wishing to be engaged in any of so-called "designated fisheries" must be licensed by the Minister of Agriculture and Forestry, and spells out principles under which such licenses are issued. Administrative ordinances specify the designated fisheries and the types of regulation under which they operate. This category includes practically all important fisheries carried out in waters far from the home islands, as well as the coastal trawl fisheries conducted by medium vessels and purse-seine fisheries by medium and

[3] The author excluded whaling from the present paper due to lack of time. The history of the whaling industry is a story of its own, and may better be dealt with as a separate topic. Two nations, Japan and the Soviet Union, are more responsible than others for the present state of baleen whale stocks. Their recovery in the Antarctic would take many years even with restrictions more severe than those currently enforced. The relative importance of whaling in the Japanese fishing industry has decreased rapidly in recent years. While the omission of the topic affects the comprehensiveness of first two sections, its inclusion would not change greatly the substance of the last section.

[4] Scholars in North America approach the question of limited entry in fisheries mainly from the point of view of economic efficiency. Application of limited entry in the Japanese fishery administration is based on much more diversified considerations. The transferability of licenses, which is an essential condition for maintaining economic efficiency under this system, has been subject to increasing constraints in Japan. While the old fishery law established fishing rights as freely transferable private properties, the new fishery law (1949) specifically prohibited transfer. The new law also prohibited in principle the transfer of licenses for offshore fisheries; in reality licenses were still transferable in most cases; but the 1963 revision of the law further restricted the transferability of licenses.

large vessels. The only major fisheries which do not fall in this category are the saury and squid fisheries, which are regulated by separate ordinances.[5] Measures to further control the operation of the designated fisheries are provided in policies for licensing which are issued by the Ministry from time to time. Licensees of each of the designated fisheries are obliged to submit reports of their operation according to the format specified by the Minister.

In short, practically all important Japanese fisheries are strictly controlled by the central government under the licensing system. The administration of fisheries under this system is, of course, subject to pressures from different groups in the industry, including large fishing companies, vessel owner associations, and fishermen's associations, but changes in fishery policies are brought about only through this centrally controlled system. The system is also effective in accommodating such changes as the government and industry consider necessary for meeting new international developments. It is also responsible for the coexistence of many different types of fishing operation for catching the same species. For example, the present pattern of Japanese trawl fishing in the North Pacific, which employs all types of trawl gear and vessels of enormous size range, could not have developed without continuous manipulation of the system by the government under pressures from various sources.

REVIEW OF SELECTED HIGH SEAS FISHERIES

Most of the important Japanese fisheries are conducted on the high seas as defined by Japan. This review includes only those which have had or are likely to have international problems. Table 1 compares the catches (round weight) of such fisheries. Some of them, particularly trawl fishing by medium vessels and purse seining, are basically coastal, but they too have international implications in relation to the fisheries of Korea, China, and the Soviet Union.

[5] These fisheries are still not subject to strict limited entry, but saury vessels and larger squid boats must be approved by the Minister and thus are subject to various regulations established by the central government.

TABLE 1.—Catches of marine fisheries, 1969.

Categories	Catch
	(Metric tons × 10³)
High seas salmon fisheries	123
Tuna and skipjack fisheries[1]	586
Trawl fisheries	
Distant water[2]	2,290
China Seas	304
Coastal	608
Mothership crab fisheries	44
Distant-water longline/gill-net fisheries[3]	27
Large and medium vessel purse-seine fisheries	1,041
Mackerel angling fishery	134
Saury fishery	51
Squid angling fishery	467
All other fisheries[4]	2,301
Aquaculture[5]	473
Total	8,449
Whaling	2,510 blue whale units
	6,668 sperm whales (head)
	627 small whales (head)

[1] Longline and pole-and-line (excluding catches by vessels smaller than 20 gross tons).
[2] Not including the China Seas.
[3] Other than tuna longline fisheries.
[4] Including inshore and coastal fisheries, as well as collection of clams (weight with shell) and seaweeds.
[5] Including oysters (with shell) and seaweeds.
Source: Ministry of Agriculture and Forestry (Japan) (1971).

TRAWL FISHERIES

Developments in the Prewar Period

A wide variety of fishing operations can be found even within one technical category, trawling. The coastal waters of Japan are crowded with a vast number of small draggers employing a great many different types of gear; over 800 Danish seiners and nearly 200 pair trawlers operate on the continental shelf and slope around and near the Japanese islands; a few otter trawlers and about 670 pair trawlers fish in the East China Sea (including the Yellow Sea); a fleet of motherships and factoryships, with trawl catchers of various types, is sent to the Bering Sea and the northeast Pacific, and a large number of independent trawlers to waters off Kamchatka and the northern Kuriles; many large stern trawlers operate in the Bering Sea and the northeast Pacific, as well as in West African waters; an increasing number of Japanese trawlers are found in the Atlantic waters off North America; and a few vessels trawl in waters off New Zealand and South Arabia. A brief review of historical sequences of development of trawl fisheries in Japan will help one understand how such a complicated pattern has emerged in this particular sector of the industry.

Different types of draggers for bottom fish have existed for several hundred years, and some of the primitive kinds can still be seen in inshore waters. The enactment of a law providing various incentives for development of offshore fisheries in 1898 and the introduction of two European-type trawlers (one imported from England and one constructed in Japan) in 1908 marked the beginning of modern trawl fishing in Japan. The fishery expanded very rapidly, the number of otter trawlers reaching 136 by 1912. This resulted in serious conflicts with inshore fishermen, prompting the government to issue trawl fishery regulations establishing large closed areas in coastal waters and to stop the application of subsidies to trawlers under the promotion law.

These measures forced otter trawlers to move into the East China Sea, leading to the discovery of new abundant resources of groundfishes, particularly highly valued porgies (sparids). The colonial administration of Korea immediately established large closed areas to shut out these trawlers from its coastal waters, thus pushing the fishery farther offshore. High costs of operation and overproduction, combined with a great demand for large vessels during World War I, resulted in a drastic reduction of trawl vessels, with only six remaining in 1918. The government, in 1917, established a new set of regulations and limited the total number of otter trawlers to 70, with a minimum size of 200 gross tons. This maximum number of 70 remained unchanged for many years for otter trawlers in the East China Sea (including the Yellow Sea).

Among the primitive methods of catching groundfishes, winddriven dragging and handhauling bottom fishing were considered most efficient in early years. With the introduction of powered vessels, the latter method developed into one somewhat similar to Danish seining. This fishery expanded very rapidly beginning in the 1910's and has since been a major source of conflicts between fishermen in inshore and coastal waters. The number of powered draggers exceeded 2,000 in the 1920's and became subject to new regulations in an attempt to control expansion and reduce conflicts with inshore fishermen. Meanwhile, the method of trawling by two vessels was introduced in 1920 and this fishery, too, began to expand at a rapid rate. Pair trawlers immediately started fishing in the East China Sea; the government then took action to control pair trawling in waters west of long 130°E under a separate set of regulations, the practice still in effect today.

Although both pair trawling and Danish seining became subject to ministerial regulations, the authority to issue licenses for these fisheries still lay in the prefectural governors. As a result, the expansion of the pair-trawl fishery in the China Sea continued, the number of its vessels reaching nearly 700 plus some 400 operating from the Japanese fishing bases in mainland China and Taiwan. In 1933, the authority to issue licenses for both pair trawling and Danish seining was transferred to the central government. The government then instituted a long-term plan to reduce these vessels, particularly Danish seiners in waters east of long 130°E, which were causing serious overfishing and conflicts with inshore fishermen. The plan was implemented for several years with some success, but with numerous problems arising from the increasing number of illegal vessels and violations of closed areas. The power to issue licenses (east of long 130°E) was transferred back to the provincial governments during World War II and remained there until 1947 when it was again given to the central government. A new cycle of various efforts to control the expansion of Danish seining and pair trawling and reduce the numbers of these vessels began in 1950-51, when the nation was still under occupation.

Regulatory measures taken during the prewar years to control the trawl fisheries of Japan established a pattern for allocating groundfish resources to different types of trawling: the stocks in coastal and nearby waters largely to the Danish-seine fishery (in the richest grounds off northern Honshu and Hokkaido) and partly to the pair-trawl fishery (in the western part of Japan); the stocks in the China Sea mainly to the pair-trawl and partly to the otter-trawl fishery; and the stocks in distant-water grounds to the otter-trawl fishery using large vessels.

Fishing in inshore waters was left largely to miscellaneous fisheries, including primitive draggers of various types. To a considerable degree, this pattern has persisted to the present, excepting some major changes in the allocation of fishing grounds in the northern North Pacific including west Kamchatka, the Bering Sea, and the Gulf of Alaska, as will be mentioned later. The coastal trawl fishery, mainly by Danish seines and partly by pair trawls, still remains the most difficult one from the point of view of fishery administration. Due to the long-established vested interests of different groups of vessels operating from different bases, the allocation of fishing grounds is extremely complex, as illustrated in Figure 1. In addition, there are closed areas around the home islands, some of which are rather extensive, different closed seasons applied in different areas, minimum depth limits in some places, as well as restrictions on the fishing bases each vessel can use for landing her catches.

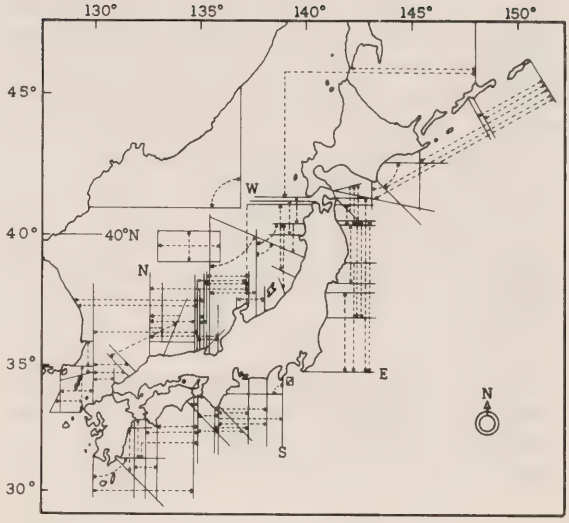

FIGURE 1.—Allocation of coastal trawl fishing grounds (from Norin Keizai Kenkyusho, 1965). Closed areas are not shown in the figure.

Post-World War II Developments

East China Sea trawl fishery.—Most of the otter trawlers and many of the pair trawlers were sunk by American submarines during the war, in most cases while serving as military transport vessels, and only eight otter trawlers were left when the war was over. To meet the serious shortage of food after the war, the government provided many incentives for reconstructing and expanding the fishing industry. The China Sea being the best trawl area in the nearby waters, the fisheries there recovered very quickly in spite of the so-called MacArthur Line limiting their fishing grounds to a narrow area of the continental shelf of the East China Sea. Numerous violations occurred and the area was later expanded slightly, but it was with the coming into force of the peace treaty in 1952 that the main fishing area became legally available to the Japanese trawl fishery.

By that time, however, 58 otter trawlers and 783 pair trawlers had been licensed, with the total fishing power far exceeding that of the prewar years. The catch per unit of effort, which had shown a remarkable recovery during the war time, started to decline sharply. Furthermore, due to international disputes with South Korea and mainland China, various restrictions were imposed on fishing operations. The expansion of the fisheries of mainland China (estimated to take roughly 70% of the total groundfish catch from the East China Sea, including the Yellow Sea) also affected the Japanese catch. Increased fishing for China Sea shrimp (*Penaeus orientalis*) improved the situation for a while, but the relative importance of the East China Sea grounds decreased rapidly as trawl fishing expanded into more distant areas, particularly the Bering Sea. Many of the otter-trawl licenses were used for obtaining new licenses for distant-water fishing by larger vessels, and there were only seven otter trawlers operating in the East China Sea by 1969. The number of pair trawlers also decreased, but to a much lesser extent. The use of pair trawlers as catchers of the Bering Sea mothership fishery also contributed toward reducing fishing pressure. Fishing in the South China Sea was also resumed in 1952 but ceased almost completely as the main fishing area, the Gulf of Tonkin, became unaccessible due to the Vietnam War.

It is important to know how the Japanese government encouraged the license holders of the trawl fisheries to move into distant waters. A policy for the otter-trawl fishery was established as early as 1950; those wishing to use otter trawlers currently licensed for fishing in the China Seas, or those proposing to abolish licenses for China Sea fishing in return for trawling in distant waters, were given priorities. A new policy on the replacement of distant-water trawl licenses (issued in 1967) is summarized in Table 2 as an interesting example of license conversion.

Coastal trawl fishery.—The trawl fisheries in coastal and inshore waters fall in two categories in the fishery administration of Japan: (1) inshore fisheries conducted by various primitive types of draggers of less than 15 gross tons each and (2) those by Danish seiners of over 15 gross tons and pair trawlers, pair trawlers being much less important except in the western part of Japan. What was referred to as the coastal trawl fishery in this section is the latter.[6] By the time the authority to license the coastal trawl fishery in waters east of long 130°E was again transferred to the central government, Japan was left with some 2,500 vessels plus a substantial number of illegal boats, and the number further increased to a maximum of over 2,800 in 1951, when a new plan for reducing them was instituted.

[6] The Japanese word for this category literally means "offshore powered trawl fishery."

TABLE 2.—Requirements for replacing a distant-water trawl vessel (in the North Pacific waters, including the Bering Sea, east of long 170°E, the Atlantic waters south of lat 40°N, and other distant areas) with a larger vessel.

Gross tonnage of existing license	Gross tonnage of new license	Licenses to be abolished
less than 550	up to 550	None
550-1,000	up to 1,000	None
over 1,000	over 1,000	None
less than 550	less than 1,000	(a) One or more distant-water trawlers, **or**
		(b) One or more Danish seiners (or pair trawlers) east of long 130°E with minimum aggregate tonnage of 50 RGT; **or**
		(c) One or more pair trawlers west of long 130°E; **or**
		(d) One or more large or medium purse seiners with minimum aggregate tonnage of 100 RGT; **or**
		(e) One or more distant-water tuna longliners with minimum aggregate tonnage of 300 RGT; **or**
		(f) One tuna mothership with three or more deck-loaded catchers.
less than 550	over 1,000	(a) Same as above; **or**
		(b) Two or more Danish seiners (or pair trawlers) east of long 130°E with minimum aggregate tonnage of 100 RGT; **or**
		(c) Same as above; **or**
		(d) Two or more large or medium purse seiners with minimum aggregate tonnage of 150 RGT; **or**
		(e) One or more distant-water tuna longliners with minimum aggregate tonnage of 600 RGT; **or**
		(f) One tuna mothership with three or more deck-loaded catchers.
550-1,000	over 1,000	(a) Same as above; **or**
		(b) One or more Danish seiners (or pair trawlers) east of long 130°E with minimum aggregate tonnage of 50 RGT; **or**
		(c) Same as above; **or**
		(d) One or more large or medium purse seiners with minimum aggregate tonnage of 50 RGT; **or**
		(e) One or more distant-water tuna longliners with minimum aggregate tonnage of 300 RGT; **or**
		(f) One tuna mothership with one or more deck-loaded catchers.

Source: Fishery Agency of Japan (1970).

Various measures were taken, including the combining of gross tonnages of smaller vessels to license a larger vessel, tighter control on illegal trawlers, compensations for giving up trawl fishing, and preferential licensing for transfer to other fisheries which were still in the process of expansion. During 1953-54, 285 licenses were transferred to other fisheries with compensations, a substantial number entering the tuna longline fishery. During 1954-56, when the salmon mothership fishery was still expanding rapidly, a large number of trawlers were converted into salmon catchers. Thus, a total of 910 licenses were taken out of the coast trawl fishery during 1953-56, with a total gross tonnage of 225,500 tons[7] (Norin Keizai Kenkyusho, 1965).

The most effective measure taken to reduce vessels operating in coastal waters, however, has been the expansion of trawl fishing grounds, which began in 1954. Danish trawling was expanded successfully into waters around the southern Kuriles, offshore banks in the Japan Sea, waters along Sakhalin and the Japan Sea coast of the Soviet Union, and, finally, waters around the northernmost part of the Kurile chain and both coasts of Kamchatka. Expansion into the northern Kuriles and Kamchatka waters marked a new era for Japanese land-based trawl fishing. By then, the Bering Sea trawl fishery, both by mothership fleets and large independent otter trawlers, was in full blast, and the mothership trawl fishery in waters off west Kamchatka had also started. A separate set of regulations, therefore, was established for fishing by trawl vessels licensed under the category of the coastal trawl fishery (see footnote 6). Great operational difficulties were encountered by the vessels engaged in fishing in these areas during the initial period, for they were largely from the existing fleet of coastal Danish seiners. Priorities for licensing were given to those having vested interests in waters around Hokkaido. Fishing area was originally defined as north of lat 48°N, east of long 148°E, and west of long 170°E, but was later expanded eastward to long 170°W with the western boundary moved to long 153°E. The fishery has grown very rapidly since 1963, and the present fleet consists of nearly 200 vessels (now called "Hokutensen," meaning vessels transferred to the north), most of them newly built stern trawlers (the upper limit of their size is set at 350 gross tons). The total catch of the fleet is nearly comparable to that of the entire mothership trawl fishery in the Bering Sea. The main fishing grounds are still in west Kamchatka and the northern Kuriles, but the amount of fish taken from east Kamchatka and the Bering Sea is also considerable. Out of the total catch of 768,000 metric tons in 1969, 670,000 tons were Pacific pollack (*Theragra chalcogramma*).

A second government plan to further reduce trawl fishing in coastal waters (the third in the history of Japanese fishery administration) started in 1962, again through the transfer of licenses to other fisheries. By that time, however, most of the other fisheries had reached or were reaching a point of saturation, and the effects of this plan were not too great. Some 30 licenses were transferred to the tuna and skipjack fisheries; a few licenses were issued for trawling in West Africa at the expense of those for coastal trawling.

Some remarks may be appropriate for the handling of the inshore trawl fishery. Emphasis of the fishery administration was on reducing the number of vessels through compensations and subsidies. Over 30,000 vessels existed in 1950, of which only 7,000 carried licenses issued by prefectural governments, the remainder being illegal vessels. The central government established policies and guidelines for the handling of this fishery, which included the definition of inshore draggers (called small bottom draggers) as vessels of less than 15 gross tons each; the establishment of nationwide limits on the total number, the combined gross tonnage, and the aggregate horsepower; the establishment of a target for reduction, etc. During the period 1956-61, a total of 2,342 vessels were scrapped to be used for "tsukiiso" (objects sunk in shallow waters to attract fish), 2,379 diverted to other

[7] The following numbers of trawl licenses were transferred to other fisheries, either converting vessels or giving up licenses in return for constructing new boats: 388 to the mothership salmon fishery as catchers, 102 to the tuna longline fishery, and 14 to the purse-seine fishery.

fisheries, and 75 converted to transport boats. But as of 1969, there still existed about 29,000 vessels, indicating that the reduction plan was not very successful. The fishery, however, is of relatively minor importance in the Japanese industry, its total production in 1969 being only 262,000 metric tons, roughly half of which consisted of shellfishes.

Mothership trawl fisheries in the Bering Sea and adjacent areas.—In the Japanese regulatory system, a mothership means a vessel with processing facilities aboard which is accompanied by one or more fishing vessels. Most of the motherships do not fish themselves, but large fishing vessels, such as factory stern trawlers, or large tuna longliners, are also defined as motherships if they are used for processing catches delivered by smaller fishing vessels. The trawl fisheries in the Bering Sea, Kamchatka, the Aleutians, and the Gulf of Alaska consist of three licensing categories: "the Northern Seas Mothership Trawl Fishery"; "the Northern Seas Trawl Fishery" conducted by independent trawlers; and "Hokutensen," mentioned above. Catches by these three categories in 1969 were 862,000 metric tons, 373,000 tons, and 768,000 tons respectively, the combined total being 2.0 million metric tons.

Trawl fishing in the Bering Sea was carried out even before and during World War II. As early as 1933, two fish meal factoryships with catchers were sent to Bristol Bay. The operation stopped after 1937 due largely to unprofitable fish meal trade. A freezer mothership operated in the Bering Sea in 1940 and 1941; a mothership operation for frozen and salted fish was conducted in waters off west Kamchatka during the war. The postwar mothership trawl fishery began in 1954 with two freezer motherships, accompanied by catcher boats, mostly otter trawlers, to produce frozen flounders, particularly yellowfin sole (*Limanda aspera*) in the Bristol Bay area. The number of freezer motherships increased to four in 1956, and a fish meal factoryship entered the fishery in 1958, as well as a mothership bottom-longline fleet. By 1961, the fishery expanded to include five fish meal factoryships (including one for processing *Atheresthes* for oil and meal) with 138 catchers, and 18 freezer motherships with 154 catchers. Three of the 18 motherships were specialized for shrimp fishing in an area near the Pribilof Islands, and eight (some of them were rather small) combined trawling, longlining (for halibut and sablefish), and gillnetting (for herring). The trawl catchers were from those licensed for fishing in the China Sea and coastal areas and included all three types: otter trawlers, Danish seiners, and pair trawlers. The Bering Sea trawl fisheries started as summer operations, but the season has since been extended, and some ships have been seen in the Bering Sea throughout the winter in the most recent years. For regulatory purposes, the Bering Sea was divided into several areas to allocate fishing grounds among different fleets taking into account their historical interests.

The next few years witnessed marked changes in the Bering Sea mothership trawl fishery. The yellowfin sole stock went down very quickly, as might have been expected for a hitherto unexploited flounder stock being subject to extremely intensive fishing, and also from past experience in waters along the Soviet coast (Kasahara, 1961). Thus, the operation of fish meal factoryships became unprofitable; this coincided with a slump in fish meal markets, both international and domestic. The number of factoryships manufacturing fish meal decreased from five (including one producing fish meal from *Atheresthes*) in 1961-62 to only two in 1963 (including one making a substantial amount of fish meal from *Atheresthes*), with the catch of flounders decreasing from 467,000 metric tons to less than 100,000 tons. A sharp decrease in the halibut catch, combined with a decline in the sablefish catch, made longlining less profitable. A sudden increase in herring production resulted in a market crisis. The shrimp fishery near the Pribilof Islands reached its peak in 1963 and declined rapidly thereafter. Meanwhile, emphasis has shifted from yellowfin sole to pollack, which is perhaps the most abundant species of commercial fish in the region. The introduction of a mechanized process to make minced pollack meat further boosted fishing for this species, and the catch has shown a phenomenal increase

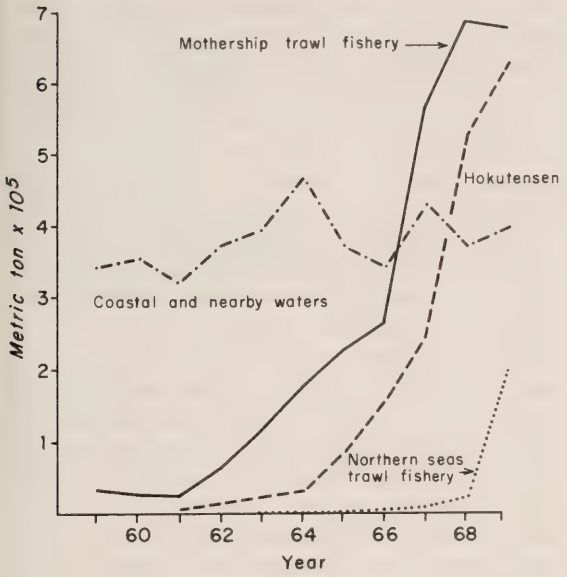

FIGURE 2.—Catches of pollack (*Theragra chalcogramma*) by Japanese fisheries, 1959-69 (from Ministry of Agriculture and Forestry, 1971).

(Figure 2). The number of vessels decreased to 12 motherships with 173 catchers by 1969, though with greater average tonnages of both motherships and catchers.

Trawl fishing in waters south of the Alaskan Peninsula began in 1960 when some of the catcher boats of a fish meal factoryship did exploratory fishing with trawls, longlines, and bottom gill nets. After 5 years of trial fishing, the government issued, in 1965, regular licenses for fishing in the Gulf of Alaska west of long 135°W under a different set of regulations. Exploratory fishing expanded into waters off British Columbia and the State of Washington. In 1967, the licensing of these vessels was combined with that of independent trawlers, mostly large stern trawlers, operating in the Bering Sea.

Independent trawlers in the northern areas.—Vessels in the category called "the Northern Seas Trawl Fishery" are licensed separately from vessels belonging to the mothership trawl fishery, but many of them are large stern trawlers sometimes accompanied by smaller trawlers (before 1967, some of these trawlers had been licensed as motherships). Emphasis is on ocean perch in the Gulf of Alaska and the Aleutians and on pollack in the Bering Sea. Distinction between this fishery and the mothership fishery is somewhat arbitrary, but it is reasonably correct to say that the former consists mainly of large stern trawlers, while the latter include motherships and factoryships accompanied by smaller trawl vessels of different types. In the Japanese regulatory system, the vessels of the former category have been licensed, since 1967, for fishing in both the Bering Sea and the Gulf of Alaska, while those of the latter category have been allowed to fish in the Bering Sea only.

Thus, the northern trawl fisheries have undergone rapid changes in the past 15 years. The exploitation of many of the important stocks has reached or exceeded the level of maximum sustainable yield, including yellowfin sole, halibut, sablefish, ocean perch, and shrimp (*Pandalus borealis*) in the Bering Sea; ocean perch in the Gulf of Alaska; and perhaps some others. Soviet fishing for flounders and ocean perch had additional effects on these stocks. The Japanese fisheries in Kamchatka and the Bering Sea are now largely dependent on one species, pollack, to be processed into fish meal and minced fish meat (on motherships and factory trawlers, as well as on land). The total amount of pollack taken in the Bering Sea and Kamchatka by the Japanese and Soviet fisheries now probably exceeds 2.5 million metric tons. Fishing intensity is still mounting, and effects of fishing are becoming apparent. The catch per unit of effort in the southeastern part of the Bering Sea has shown a decrease, and the average size and age of fish also have decreased. Fishing grounds have spread over the deeper portions of the central Bering Sea shelf. Further improvements in the method of catching pollack are under study, for pollack occur not only near the bottom of the shelf and upper slope but also in midlayers of deeper waters. The maximum level of exploitation will be reached fairly soon if it has not been already. There may be a further increase in the Japanese share of ocean perch in the Gulf of Alaska if Soviet efforts are drastically reduced. Japan has not fished for hake to any

extent, but the hake stocks have also been fished intensively by the Soviet Union. The potential of the herring stocks in the eastern Bering Sea, the cod stocks in the Bering Sea, and the sablefish stocks in southern areas are not well known, but it is not very likely that the catch of any of these species will substitute for a substantial portion of the present catch of pollack. As domestic markets for fish meal and minced fish meat remain strong, fishing pressure on pollack is bound to increase further.[8]

Certain actions by the Japanese government appear necessary in order to avoid a possible economic disaster: full assessment of the status of important stocks in the Bering Sea, Kamchatka, and the Gulf of Alaska; the establishment of catch quotas for pollack and a few other important species, in each of the three regions, in collaboration with the Soviety Union if feasible; and reallocation of fishing grounds among different sectors of the industry to make best use of the allowable catches. International problems arising from the development of trawl fisheries in the northern Pacific will be summarized in a later section.

Trawl fishery off west Africa.—The trawl fisheries in areas other than the northern North Pacific are licensed under the category "Far Seas Trawl Fisheries." The most important of these is the fishery along the west coast of Africa. The Soviet Union started trawl fishing off northwest Africa in the late 1950's and a few Japanese trawlers began fishing in 1959. In addition to local African vessels and Spanish and Portuguese boats, trawlers from a large number of non-African countries have fished in waters along the west coast of Africa. They include the Soviet Union, Japan, Poland, Italy, Israel, Greece, France, East and West Germany, Norway, Bulgaria, Romania, Belgium, South Korea, and China (Taiwan). The best trawl grounds occur in waters off northwest Africa and southwest Africa, more or less corresponding to the areas of strong coastal upwelling, that is, along Spanish Sahara and Mauritania in the north, and Angola, South-West Africa, and South Africa in the south. Trawl fishing in west Africa is very selective as to species caught, except in the south where hake predominate in the catches of most fleets. Japanese fishing has been mainly for cuttlefish (mongoika), octopus, and porgies (sparids) in the north; hake, porgies, and jack mackerel around the Cape; and mostly hake in waters off Angola and South-West Africa.

In the early years, the Japanese government was reluctant to increase the number of licenses for fishing in Africa. As it became obvious that other nations were intensifying their effort rapidly, the government relaxed its licensing policy and the number of vessels increased to about 70 in 1967, most of them large stern trawlers. The total catch in 1969 was roughly 240,000 metric tons. The Japanese fleet has been facing difficulty due to a decrease in the catch per unit of effort of high priced species and the expansion of national jurisdiction by the coastal states.

Vessels operating in the north are mostly based in Las Palmas, and Cape Town is the main fishing base for those in the southernmost area. Catches have been sorted out at these bases for transshipment to Japan or export to other nations. Ghana, Italy, Nigeria, Greece, and Romania have been among the main importers of trawl fish caught by Japan. Substantial amounts have also been landed directly in African ports for local sales—Lagos, Monrovia, Tema, Freetown, etc.

Trawl fishery in the North Atlantic.—Japan has made a substantial effort to develop a trawl fishery in the main international fishing area of the northwest Atlantic, particularly off Newfoundland, but the attempt has been an almost complete failure. She has, however, established a fishery in waters farther south, mainly off New York, as an attempt to divert seasonally some of the vessels operating in African waters. Some trawlers now plan to stay there almost year round. Main species are squid, butterfish, and argentine, with a total catch of 9,000 tons in 1969. Exploratory fishing has also been con-

[8] A 5,000-ton factory stern trawler has come into operation and several more in the same class are under construction, all to fish in the northern North Pacific. The Soviet Union has greatly increased fishing for pollack. South Korea has also begun pollack fishing in the northern areas.

TABLE 3.—Catches (metric tons × 10^3) of trawl fisheries in different categories, 1959-69.

Categories	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
Northern seas mothership trawl fishery[1]	169	472	639	534	338	438	404	454	778	844	862
Northern seas trawl fishery[2]	2	--	4	6	18	29	[3]62	[3]97	123	193	373
Hokutensen[4]	--	--	19	35	48	69	130	211	319	618	768
Atlantic and other seas	5	13	34	53	97	130	119	182	281	286	287
West of 130°E (China Seas)	357	368	375	331	345	302	325	334	338	326	303
Coastal trawl fisheries[5]	521	632	632	629	594	655	677	574	528	583	572
Inshore dragnet fisheries	239	230	213	215	208	209	230	253	269	276	259

[1] North Pacific and adjacent seas. Including small catches by gill net and longline.
[2] North Pacific and Bering, east of long 170°E.
[3] Including catches of the mothership fishery in the Gulf of Alaska.
[4] North of lat 48°N, east of long 153°N and west of long 170°W.
[5] East of long 130°E. "Offshore trawl fisheries" in Japanese terminology (see text).
Source: Ministry of Agriculture and Forestry (Japan) (1971).

ducted in waters off Florida. Although the New York fishery might expand further, it is unlikely to become a major trawl fishery comparable to that in Africa. Fishing in the North Pacific remains most attractive for large stern trawlers, and there are at present no plans to develop a major Japanese fishery in the main international fishing grounds of the northwest Atlantic.

Trawl fisheries in other areas.—Trawl fishing grounds in waters off New Zealand and Australia (west coast) were known to Japanese companies even before the war. Fishing after World War II started around 1959 largely for porgies (sparids). The trawl fishery off Australia has never developed to an important one, while trawling off New Zealand has expanded recently, the total catch in 1969 being 26,000 tons. Initially, the catch was mainly porgies (similar to Japanese "tai," *Chrysophrys*), but now barracouta (*Leionura*) is caught in large quantities, in addition to jack mackerel and porgies.

A Soviet fleet and some Greek trawlers fished in the Gulf of Aden along the South Arabian coast, before the closing of Suez, as well as in waters off northeastern Somalia. Soviet trawlers are fishing again along the Arabian coast. Japanese trawling in the Gulf of Aden began in 1966 for cuttlefish, porgies, and some other species; eight trawlers fished in 1967, with a total catch of 12,000 metric tons (Suisan-sha, 1970). This again has not developed to a major fishery.

Table 3 summarizes catches of the different trawl fisheries described in this section for the period 1959-69.

Mention should be made of the shrimp fisheries conducted by Japan in foreign countries after World War II (the Japanese did some shrimp trawling in Mexican waters during the prewar years). The oldest of these is the one along the northeast coast of South America. Shrimp fishing there has been developed mainly by American operators since about 1955. The establishment of a shrimp processing plant in Georgetown (Guyana, then British Guiana) marked the beginning of large-scale shrimping in that part of the world. Processing plants have since been built in Paramaribo, Cayenne, Port of Spain, Barbados, Belém, etc., and several hundreds of American shrimp boats are operating under various arrangements with the local governments and business groups. Shrimp grounds are generally between the Orinoco River mouth and the Amazon River mouth, with best areas located along the Guianas and northern Brazil.

Japan started shrimping in the region around 1959 and developed a small fishery based in Paramaribo. The Japanese government tightly controlled shrimping in that region for unknown reasons until 1967 when it relaxed restrictions. The total number of vessels licensed reached 72, including 50 land-based vessels and 22 vessels conducting mothership-type operations. Main bases are Georgetown, Paramaribo, and Port of Spain. Initially, shrimp trawlers built in Japan were used, but practically the entire fleet now consists of standard Gulf of Mexico shrimp trawlers constructed in the United States. The Japanese firms have formed a joint company apparently for the purpose of negotiating local arrangements.

Japan has also engaged in joint ventures for shrimp in India, Australia, Madagascar, Malaysia (Sarawak), and other countries. Recent

emphasis is heavily on shrimp ventures in Indonesian waters. After conducting exploratory fishing, several companies now plan to establish facilities at shore bases. The best grounds are along the north coast of Sumatra, the south coast of Borneo (Kalimantan), and the south coast of West Irian.

SALMON FISHERIES

Japanese salmon fishing from the Russian territory began in the latter half of the 19th century. After the Russo-Japanese War, the two governments entered into negotiations on the question of Japanese fishing rights along the Russian coasts. The resulting treaty of 1907 (went into force in 1908) greatly facilitated the expansion of Japanese fishing activities from the Russian territory. The treaty recognized the rights of the Japanese to fish along the Russian coasts of the Japan Sea, the Okhotsk Sea, and the Bering Sea, including the entire coastline of Kamchatka, the most important salmon-producing area in Asia. A large number of lots for salmon trap fishing were distributed, by auction, between the Russians and Japanese (Leonard, 1944; Kasahara, 1961).

After the Russian Revolution, a temporary arrangement was made until a new treaty was signed in 1928 after long negotiations. The new agreement modified the arrangements of the 1907 treaty, but the rights of the Japanese to fish from the Russian territory were reestablished. The Soviet government thereafter tried to expand the fishing activities of its nationals by reducing the proportion of lots leased to the Japanese, resulting in continuous controversies and negotiations. The amount of Japanese fishing for salmon in the Soviet territory was reduced drastically after 1941, when the Pacific War broke out, and the entire fishery came to an end in 1944.

While negotiations for the allocation of fishing lots were going on between the two governments, the Japanese began to engage in a mothership-type salmon fishery in waters off Kamchatka (motherships were anchored outside the territorial sea). The fishery lasted from 1929 to 1942. More important was the development, during the 1930's, of drift net and trap fishing based in the northernmost islands of the Kurile chain,[9] which intercepted a large number of salmon on their way to the streams in the Kamchatka Peninsula and other areas of Russia. (See Kasahara, 1963, for catch statistics.) It appears peculiar that such new developments, which no doubt had substantial effects on inshore salmon catches, did not result in a serious controversy during the prewar period. If these offshore fisheries had continued, difficult problems would have developed not only between Japan and the Soviet Union but also between different Japanese fisheries catching salmon. In any case, these developments clearly indicated what the Japanese might do if they were excluded from fishing salmon in inshore waters.

Article 9 of the San Francisco peace treaty states, "Japan will enter promptly into negotiations with the Allied Powers so desiring for the conclusion of bilateral and multilateral agreements providing for the regulation or limitation of fishing and the conservation and development of fisheries on the high seas." The North Pacific fishery treaty was signed on May 9, 1952, immediately after the peace treaty entered into force on April 28 of the same year.

Expecting the abolishment of the so-called MacArthur Line restricting Japanese fishing grounds during the occupation period, the Japanese government issued, early in 1952, its policies on the resumption of the high seas salmon fishery. Three motherships with 50 catchers and 12 scouting boats were licensed. Each of the three biggest fishing companies, Taiyo, Nippon Suisan, and Nichiro, was authorized to operate one mothership, with Danish seiners from the coastal trawl fishery east of long 130°E (mentioned previously) employed as catcher boats. The fleet left Japan just 3 days after the peace treaty came into force. Although the North Pacific treaty had not been ratified by Canada, fishing was authorized only in waters west of long 175°W and between lat 48°N and 55°N; waters off Kamchatka and the northern Kuriles were avoided. The fishery differed entirely from

[9] The entire Kurile Islands and the southern half of Sakhalin belonged to Japan until the end of World War II.

the mothership fishery before World War II, which was conducted in waters very close to the Kamchatka Peninsula. The result was a smashing success, and this set a pattern for further development of the mothership salmon fishery on the high seas. The land-based drift-net fishery, too, operated in a large area of the high seas; 1,500 drift netters fished for salmon, mostly pink salmon heading for Soviet streams. The government issued new regulations for the land-based drift-net fishery.

By 1955, the mothership expanded to 14 motherships, including 2 in the Okhotsk Sea, with 344 catchers and 58 scouting boats; the land-based drift-net fishery was conducted by 325 larger vessels (over 30 gross tons) licensed by the central government and more than 1,200 smaller vessels licensed by the prefectural governments. The mothership fishery took 64 million salmon (in number of fish) and the land-based fishery 47,000 metric tons (in round weight). Japan had planned to increase the number of motherships to 19 in 1956 with a corresponding increase in the number of catcher boats.

In February 1956, the Soviet Union took unilateral action to restrict high seas salmon fishing in the northwest Pacific (west of long 170°E). The two governments entered into negotiations for a fishery treaty, which was concluded on May 15 and entered into force a few months later. The diplomatic relations between the two nations were restored later in the year. The new fishery treaty set forth a wide variety of regulations, including large closed areas, closed seasons, catch quotas, restrictions on fishing gear, and arrangements for enforcement (a system of inspection by the Soviet authorities). Many changes have taken place since then, including the development of a large longline salmon fishery on the high seas and a substantial salmon fishery in the Japan Sea, expansion of the regulatory area, changes in the allocation of fishing grounds and catches between different Japanese fisheries, the closure of the entire Okhotsk Sea, and continuous modifications of the domestic regulations to meet the international situation. The pattern of salmon fishing as of 1969 is summarized in Figure 3. The number of catchers has been reduced substantially by transferring their licenses to the tuna longline fishery and the northern trawl fishery. Due to expansion of the regulatory area and a continuous reduction of the catch quota under the treaty, which was considered necessary by the Soviet Union for conservation, the total take of salmon by Japan (including small amounts of salmon destined for Japanese streams) decreased from 197,000 metric tons in 1958 to 141,000 metric tons in 1969 (Ministry of Agriculture and Forestry, 1971).

In short, the expansion of the Japanese high seas salmon fisheries came to an end already in the 1950's when regulatory measures under the Japan-Soviet fishery treaty were applied to practically all areas of the northwest Pacific in which salmon were found. Offshore fishing must have had adverse effects on the salmon stocks in general, but the exact nature and extent of such effects are not well understood from the data and information exchanged through the Japan-Soviet fisheries commission.

The eastern boundary of the offshore salmon fishing grounds was established at long 175°W under the North Pacific treaty. In spite of extensive research conducted on the offshore distribution of salmon, resulting in a wealth of scientific information, and continuous hard negotiations between the national sections of the North Pacific fisheries commission, this provisional line has remained unchanged to date. Substantial quantities of Bristol Bay sockeye salmon have been taken by the Japanese mothership fishery in years of large runs, but none of the three parties has seriously considered the termination of the treaty, which could have been done at any time after 1963 with 1 year's advance notice. Thus, the provisional line drawn in 1952 has proved to be a good political compromise as far as these three countries are concerned.

CRAB FISHERIES

Three species of king crab (*Paralithodes*) and tanner crab (*Chionoecetes* spp.) have been exploited by the high seas crab fisheries in the northern North Pacific. The most important are the true king crab (*P. camtschatica*) and the tanner crab. Abundant resources occur in

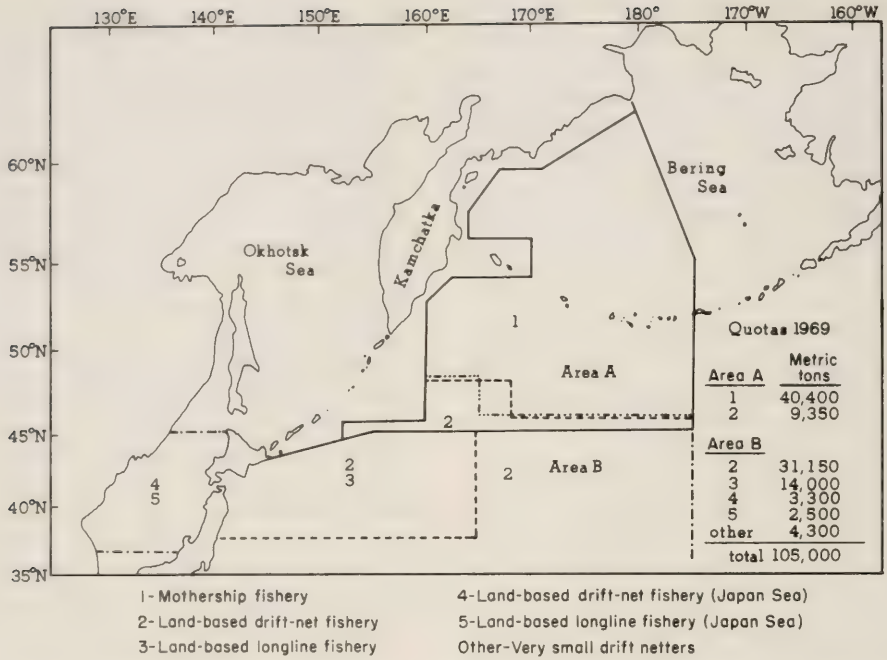

FIGURE 3.—Allocation of high seas salmon fishing grounds, 1969 (from Suisan-sha, 1970).

waters off northern Japan and Sakhalin, Kamchatka (particularly the west coast), the eastern Bering Sea, and the east Aleutian-Kodiak area. Land-based crab fishing for manufacturing canned crab dates from 1905; it expanded from Hokkaido to Sakhalin and the northern Kuriles. Exploratory attempts for fishing with motherships began in the 1910's along the west coast of Kamchatka, and commercial fishing of this type started in 1921. Stimulated by growing international markets for canned crab, the fishery expanded rapidly and the government, as usual, issued king crab mothership fishery regulations in 1923. The number of motherships was limited to 18 in 1927. Attempts were also made to develop crab resources along the east coast of Kamchatka without much success. The mothership crab fishery in Bristol Bay began in 1930 and continued until 1939 (no fishing in 1931). It never developed to a major fishery before World War II, only one mothership operating in most years. Crab fishing from the Russian territory was first conducted in connection with salmon fishing, but it was in 1920 that an official arrangement was made between the Russian and Japanese governments to permit Japanese crab fishing from the Russian territory (west coast of Kamchatka) under Russian regulations. (The Japanese salmon and crab fisheries from the Russian territory were practically monopolized by one company, Nichiro.) Both mothership crab fishing and land-based fishing employed tangle nets; motherships carried small powered boats called "kawasaki-sen" to do the fishing and were equipped with canning lines to process crabs aboard.

As in the case of the salmon mothership fishery, the Japanese government issued its policies on the resumption of the Bristol Bay crab mothership fishery prior to the entering into force of the peace treaty in 1952. Because of political repercussions from the United States, no fishing was authorized in that year, and only one mothership was licensed for 1953 as a joint operation by the three biggest fishing companies, Taiyo, Nippon Suisan, and Nichiro. Specific regulations were issued to limit the number of deck-loaded boats as well as self-navigating fishing

vessels (for scouting and setting nets), the amount of canned crab produced, and the amount of tangle nets used. This form of operation continued until 1959 without a major expansion, except for a substantial increase in the production quota in 1959. A second mothership fleet was authorized to operate in the Bering Sea in 1960 to produce frozen crab. The fishery thereafter grew very rapidly until 1964, when a record catch of over 10 million crab was made.

Having declared exclusive rights to exploit king crab resources under the 1958 continental shelf convention (entered into force in 1964), the United States initiated, in 1964, negotiations with Japan concerning the crab fishery in the eastern Bering Sea. Since then, the Japanese catch has been reduced continuously under international agreements between the two governments.

The first Soviet mothership crab fleet entered the eastern Bering Sea in 1960, resulting in direct competition with the Japanese fishery. The U.S. crab fishery in the Bering Sea remained of minor importance through 1963, with no fishing conducted in some years. U.S. vessels from Kodiak and adjacent areas moved into the Bering Sea in 1964 and their catch has been increasing since then. Traditionally, Japanese fishing was by tangle nets and U.S. fishing in waters south of the Peninsula was by pots (some U.S. vessels used to trawl for crab in the Bering Sea). Now pot fishing is conducted both by the Japanese and the Americans, complicating the situation further. The Japanese and the Soviets have also developed a system of allocating tangle-net fishing grounds between their fleets. As the eastern Bering Sea king crab stock began to show signs of depletion, Japan intensified fishing for tanner crab, which is also very abundant in the eastern Bering Sea. Tanner crab fishing is now as important as king crab fishing and, through a quota, under control by the Japan-United States agreement.

The Japanese mothership crab fishery in waters off the west coast of Kamchatka (the most important king crab fishing area) was resumed in 1955, before the conclusion of the Japan-Soviet fishery treaty, and became subject to the provisions of the treaty in 1957, which covered two species of king crab, *P. camtschatica* and *P. platypus*. The regulations under the treaty were applied to both the Japanese and Soviet mothership fleets, with Japanese share decreasing since 1965. As a party to the 1958 continental shelf convention, the Soviet government declared, in 1968, its exclusive rights to natural resources of the continental shelf adjacent to its territory. Although Japan was not a member of the convention, she agreed, in 1969, to negotiate a separate arrangement for crab fishing, which resulted in a 1-year agreement specifying the catch limits of different species of crabs for the Japanese fisheries in designated areas, as well as the number of motherships or fishing vessels to be used for crab fishing. Thus, not only crab fishing on the west coast of Kamchatka for king crabs but also tanner crab fishing in the western Bering Sea, as well as fishing for a variety of crabs in waters off the southern Kuriles and Sakhalin became subject to regulation. The agreement has since been revised year after year. The complex legal arrangements for crab fishing in the northern North Pacific will later be reviewed in some detail.

TUNA FISHERIES

Japan had a tuna fishing fleet consisting of about 2,000 vessels before the war, but they were largely small boats operating in waters not too far from the home islands. Pole-and-line skipjack fishing was much more important than longline tuna fishing, with the bulk of the vessels carrying out both.[10] Skipjack fishing was also conducted from various bases in the present Trust Territory of the Pacific Islands. Although tuna are caught by other types of gear, particularly purse seine (also by traps in small quantities), the Japanese tuna industry consists largely of the longline tuna fishery and the pole-and-line skipjack fishery, the latter taking a sub-

[10] A complete account of the Japanese tuna industry up to about 1962 is given in Masuda (1963, in Japanese). In the Japanese language, skipjack ("katsuo") is distinguished from larger tunas ("maguro"). Substantial quantities of billfishes and swordfish are also caught by tuna longline; they are generally called "kajiki."

stantial amount of albacore also. While a number of vessels still conduct both types of fishing, distant-water tuna fishing is almost exclusively by longliners. The main grounds of the skipjack fishery are still in waters relatively close to the Japanese islands, including those adjacent to the Trust Territory of the Pacific Islands. In the licensing system of Japan, tuna and skipjack fisheries have always been combined, mainly because the tuna longline fishery originally developed as a part-time operation of skipjack pole-and-line vessels.

Under the new fishery law (1949), all tuna and skipjack vessels larger than 20 gross tons were required to obtain licenses issued by the Minister of Agriculture and Forestry, thus coming under full control by the central government. They were further divided between those below and above 100 gross tons, called the "medium vessel tuna-skipjack fishery" and the "far seas tuna-skipjack fishery," respectively. In 1953, after abolishment of the MacArthur Line, the Japanese government enacted a law to provide a preferential treatment of licenses for larger tuna vessels (over 70 gross tons) until 1955, as an attempt to develop tuna fishing in waters farther from the home islands. The law encouraged licensees to replace small vessels with new larger vessels and also accommodated the entry of operators from other fisheries, particularly the coastal trawl fisheries. A further policy was issued in 1955, allowing vessels in the category of the medium vessel tuna-skipjack fishery to combine their gross tonnages to obtain licenses for new larger vessels under the category of the "far seas tuna-skipjack fishery." A number of licenses were also transferred from the salmon fishery to the tuna fishery as the number of vessels in the former had to be reduced as a result of the Japan-Soviet fishery treaty.

Further changes were made thereafter to establish a new category for the mothership-type tuna fishery with deck-loaded catchers and to abolish the distinction between the above-mentioned two categories, with vessels less than 40 gross tons removed from the licensing system. As fishing by vessels less than 40 gross tons became free of license limitations, the number of such boats increased at a rapid rate with their fishing grounds expanded to both sides of the equator.[11] The government in 1963 put the licensing of tuna vessels over 20 tons again in two categories divided at 50 gross tons, which was later raised back to 70 gross tons. In short, the government encouraged the tuna fishery (particularly longline fishing) to expand into waters farther from Japan with larger vessels, and also used the tuna fishery for reducing the number of licenses in other overcrowded fisheries.

This policy contributed to the rapid expansion of tuna longline fishing grounds. By 1960, the Japanese tuna fleet had covered the main longline fishing grounds in the North and South Pacific and the Indian Ocean. Longlining in the Atlantic started in 1957 and the major Atlantic tuna grounds had been fished by 1962. Fishing grounds further expanded thereafter, though more gradually. Fishing for southern bluefin tuna ("minamimaguro," *Thunnus maccoyii*) in waters off New Zealand and southern Australia has been intensified greatly in recent years since new freezing equipment was introduced to produce frozen tuna meat of highest quality. The strength of the Japanese tuna longline fishery as a whole reached its highest point in 1962; the industry has been on the decline since then, with Taiwan and South Korea increasing their shares. Japan still has advantages over Taiwan and other longline fishing nations in some respects. It has a tremendous trade network developed by trade companies to market tuna anywhere in the world; the catches of many Taiwanese and South Korea longliners are transshipped through foreign bases under the management of these Japanese trade companies. High-quality bluefin is sold in Japan at a fantastic price. Japan also has strong markets for bigeye, billfishes, and other species that have no or very limited markets in the United States. But as far as tuna production is concerned, Japan's share will decrease further. In addition to Taiwan and Korea, Ryukyu has a sizable longline fleet, which will become part of the Japanese tuna industry when Okinawa is returned to Ja-

[11] In the Japanese practice, the actual gross tonnage of a vessel is substantially greater than the registered gross tonnage (RGT) in most cases.

pan. Cuba operates a small fleet in the Atlantic; the Soviet Union has a mothership tuna fishery of relatively minor importance. Most of the attempts by other nations to develop a tuna longline fishery have failed. (Venezuela has a fleet of small longliners. The fishery is protected by regulations prohibiting the import of tuna and tuna products.)

Tuna longlining is conducted in a variety of ways. The bulk of Japanese vessels still operate from Japan, but a large number also use foreign bases. In the South Pacific, catches are delivered to American Samoa, Espíritu Santo (New Hebrides), and Fiji. Penang and Port Louis (Mauritius) have been the main bases in the Indian Ocean. Mombasa is a base established recently. Vessels operating in the Atlantic have delivered their catches to such ports as Las Palmas, Abidjan, Cape Verde Islands (Portuguese possession), Tema, Cape Town, Port of Spain, etc. St. Martin Island in the Caribbean has been an important base in recent years. (See Broadhead, 1971, for a description of international tuna trade.) Many of these foreign transshipping bases now receive more fish from Taiwanese and Korean vessels than from the Japanese boats. Mothership-type tuna longlining has also been conducted both with self-navigating catchers and with deck-loaded boats, but the former type has ceased to exist. The mothership fishery with deck-loaded catchers has developed largely in the last 15 years although some experiments were conducted even before World War II. Each mothership, which also does fishing in most cases, carries 1 to 8 fishing skiffs. The catches of the different types of tuna fisheries are compared in Table 4.

It has been demonstrated that the catch per unit of effort in any region quickly decreases as the amount of longline fishing increases. It is also apparent that the total longline catches of yellowfin, albacore, bigeye, and bluefin tunas from the world ocean will not show substantial increases as fishing is further intensified although the proportions taken by the different longline fishing nations will change further.

The pole-and-line skipjack fishery operates relatively close to Japan, but a large number of vessels now fish in waters around the Trust Territory of the Pacific Islands (from bases in Japan). The fishery also takes a substantial amount of albacore; some vessels still conduct both pole-and-line skipjack fishing and tuna longlining.

Some tunas and skipjack are caught by purse seiners in waters close to Japan. A few tuna seiners have been operating in West Africa. The Japanese have also been trying to establish a purse-seine fishery in the eastern tropical Pacific, so far without success.

OTHER FISHERIES

Some of the other fisheries, principally those conducted around the Japanese islands, have had or are likely to have some international implications. These include, among others, the purse-seine fisheries for coastal pelagic fish, the saury fishery, and the squid fishery. The kelp fishery around the southernmost islands of the Kurile chain is also an international issue.

Most of these fisheries depend on the resources of coastal pelagic species in waters around Japan. The combined catch of main coastal pelagic species in *temperate waters*, including anchovy (*Engraulis*), sardines (*Sardinops* and *Etrumeus*), jack mackerels (mainly *Trachurus* and *Decapterus*), mackerels (two species of *Scomber*), saury (*Cololabis*), yellowtail (*Seri-*

TABLE 4.—Catches (metric tons × 10^3) of Japanese tuna fisheries.[1]

Years	Oceans			Longline					Pole-and-line[4]	Seine	Trap	Others
	Pacific and Indian	Atlantic	Total	Home-based	Foreign-based[2]	Atlantic	Mother-ship[3]	Total				
1962	395	55	450	275	23	55	51	404	21	16	3	6
1969	299	33	333	220	12	13	31	275	43	8	2	5

[1] Bluefin, southern bluefin, albacore, bigeye, yellowfin, and some small tunas.
[2] Other than Atlantic.
[3] With deck-loaded catchers.
[4] Mainly albacore.
Source: Ministry of Agriculture and Forestry (Japan) (1971).

ola), and common squid (*Ommastrephes*), was about 2.7 million metric tons in 1969[12] out of the total Japanese catch of all marine fishes and shellfishes of 7.7 million tons (round weight, not including aquaculture), indicating the importance of this group of species.

After the catastrophic decline of the sardine catch (Kasahara, 1961) fishing for other pelagic species, particularly those mentioned above, became increasingly intensive. Saury fishing with "boke-ami" (stick-held lift net with fish-attracting light) started in 1947, and the catch soon reached to a level of 500,000 metric tons a year. It has been on the decline since 1962 (Figure 4). The catch of jack mackerels started to climb sharply around 1949, with some signs of an increase in abundance, and exceeded 500,000 tons (*Trachurus* alone) in 1960; it has since been decreasing. The mackerel yield began to rise also in the late 1940's and it is still going up. The catch of anchovies has been fluctuating at around 300,000 to 400,000 tons a year since the early 1950's (Figure 5). The yield of squids, mostly common squid, also rose markedly after the war and has shown rather violent fluctuations in recent years (Figure 6). All of these species have been under intensive fishing for the last 20 years or so, but their catch trends have been rather different from each other. A variety of biological problems are involved, many of which are poorly understood. The catches of the Soviet Union and South Korea are also indicated in the figures wherever data are available.

The rapid development of fishing for mackerel and jack mackerel resulted in a serious conflict with the South Korean fishermen, which will be mentioned later. The Soviet vessels have been catching an increasing amount of mackerel in waters off northern Japan. The decline of the saury catch has prompted some of the Japanese companies to apply for exploratory fishing in waters of the eastern Pacific, particularly off Canada and the United States. In 1969, about 38 applications were approved by the Japanese government, but only about half of them conducted fishing, mainly off Canada and the United

[12] Perhaps 3 million metric tons if miscellaneous species are included.

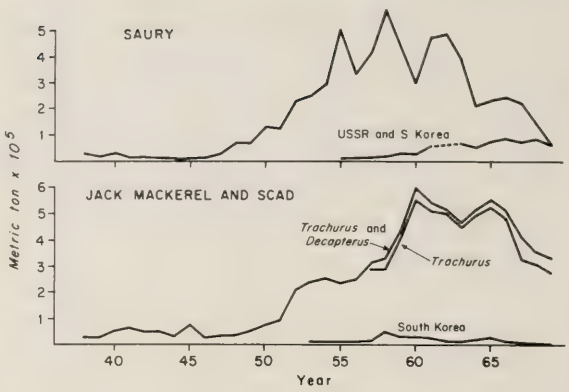

FIGURE 4.—Catches of saury and jack mackerel in Japan, 1938-69 (from Ministry of Agriculture, 1962-1971).

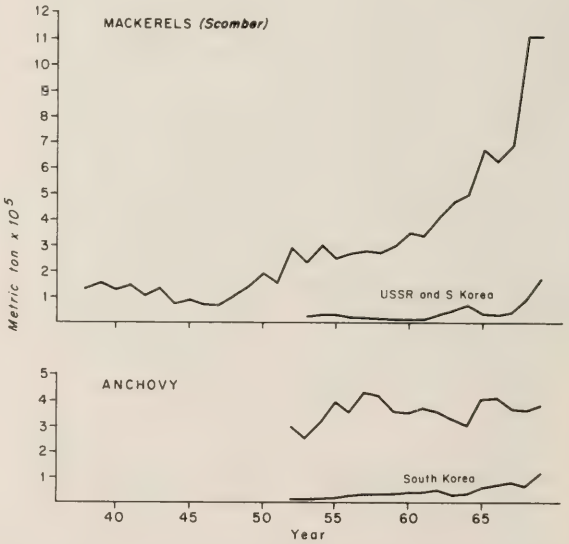

FIGURE 5.—Catches of mackerels and anchovy in Japan, 1938-69 (from Ministry of Agriculture and Forestry, 1962-71). USSR mackerel catches are only rough estimates.

States. The result was not very encouraging, but exploratory fishing will continue, depending to some extent on the saury catch in waters off Japan (there was a slight recovery in 1970) and the trend of the saury market. The Soviet catch of saury in waters off northern Japan and the Kuriles, in competition with the Japanese, has become substantial in recent years. A complicated international situation has developed con-

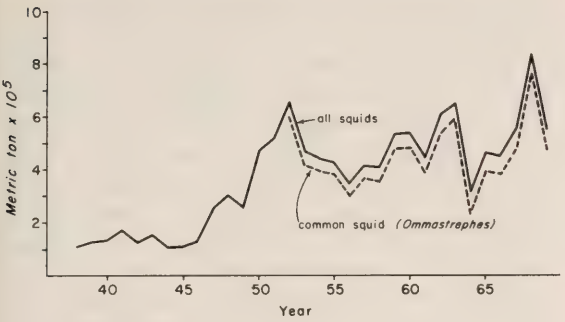

FIGURE 6.—Catches of squids in Japan, 1938-69 (from Ministry of Agriculture and Forestry, 1962-71).

cerning the Japanese kelp fishery in inshore waters around the southernmost islands of the Kurile chain occupied by the Soviet Union.

At the moment, squid fishing by Japan has no international implications, but the squid resources in the North Pacific appear to be among the most important potential resources for the future. Since species similar to the common squid occur in great quantities in the eastern Pacific, in waters of national jurisdiction as well as on the high seas, the exploitation of squid might become an international issue in the future. (A survey of squid resources off California is now under consideration in Japan.)

INTERNATIONAL ARRANGEMENTS

INTERNATIONAL PROBLEMS ARISING FROM THE POSTWAR EXPANSION OF JAPANESE FISHERIES

Period of Occupation

International conflicts arising from the prewar development of Japanese fisheries are summarized by Leonard (1944). Japan was involved in four major international issues concerning fisheries: the Russo-Japanese controversy; the North Pacific fur seal controversy; international problems of Antarctic whaling; and the Alaska salmon fishery issue. Except for the first one, which was resolved by the war itself, these controversies remained unsettled. The nature of the problems will be reviewed retrospectively in connection with postwar developments.

The Japanese fishing industry was half destroyed during the war with most of the larger fishing vessels sunk by American submarines. Large fisheries developed by the Japanese in Korea, Taiwan, Sakhalin, and the Kurile Islands were completely lost as these areas became independent or were taken by the Soviet Union. Japan also lost historical rights to fish in Kamchatka and other Far Eastern areas of the Soviet Union. The total catch decreased to less than 2 million metric tons in 1945, the last year of the war. The rebuilding of the industry started as early as 1946. Pressed by the immediate need to feed the nation and to earn foreign exchange, the government provided tremendous incentives for the industry to expand as fast as possible.

The first international problem faced by Japan was the area restriction imposed on her fisheries by the Allied Powers. Both government and industry strongly urged the expansion of the authorized fishing area. The area was expanded to the west to include a substantial portion of the east China Sea continental shelf (1946) and to the east and the south to permit tuna and skipjack fishing in vast areas of the western Pacific (1946, 1949, and 1950). As of 1950, however, the authorized area was still restricted to waters north of the equator and west of long 180°, except for Antarctic whaling, which was resumed in 1946.

Pressure was mounting in the United States and Canada to restrict Japanese high seas fishing as a condition for the restoration of diplomatic relations. Two international problems of the prewar period should be mentioned in this connection. During 1936-38, Japanese exploratory fishing vessels appeared in the eastern Bering Sea and caught salmon. This triggered tremendous reactions from the American industry, administration, and Congress. Legislation was introduced in Congress calling for the exercise of jurisdiction on the high seas, and a variety of views were expressed on the legal basis for taking such an action. The Japanese government finally agreed to keep its vessels from fishing salmon in waters off Alaska, without prejudice to Japanese rights under international law

(Leonard, 1944). The question of whether the United States had an exclusive right to exploit the salmon stocks was not discussed in legal terms, but the general feeling among the American people was that these salmon really belong to them. The above instance had a great impact on the attitude of the Americans toward the development of Japanese high seas fisheries after the war. Another prewar issue, which affected the reputation of Japan as a fishing nation, was the abrogation of the 1911 fur seal treaty by Japan.[13] The Japanese government claimed, without substantiating scientific evidence, that the increase in the fur seal population as a result of protection provided by the treaty was causing serious damage to their fisheries.

As the question of Japanese fishing became a very serious issue which might delay the conclusion of the peace treaty, the United States and Japan agreed to deal with problems further in an exchange of letters between the Japanese Prime Minister (Shigeru Yoshida) and the American Ambassador (John Foster Dulles) in February 1951. The prime minister's letter stated, ". . . the Japanese government will, as soon as practicable after the restoration to it of full sovereignty, be prepared to enter into negotiations with other countries with a view to establishing equitable arrangements for the development and conservation of fisheries which are accessible to the nationals of Japan and such other countries.

"In the meantime, the Japanese government will, as a voluntary act, implying no waiver of their international rights, prohibit their resident nationals and vessels from carrying on fishing operations in presently conserved fisheries in all waters where arrangements have already been made, either by international or domestic act, to protect the fisheries from over-harvesting, and in which fisheries Japanese nationals or vessels were not in the year 1940 conducting operations. Among such fisheries would be the salmon, halibut, herring, sardine, and tuna fisheries in the waters of the Eastern Pacific Ocean and Bering Sea." (Fishery Agency of Japan, 1953.)

[13] A notice was given in 1940 and the treaty terminated in 1941. To continue protective measures in the northeast Pacific, a provisional agreement was made between the United States and Canada.

The question of fur seal was dealt with in an exchange of memoranda in April 1951. The Japanese memorandum stated, "The Japanese government has no objection to the interpretation of Prime Minister Yoshida's letter of February 7, 1951, as extending to pelagic fur sealing. That is to say, pending the conclusion of a new convention on the subject after the coming into force of a peace treaty, the Japanese government will, implying no waiver of their international rights, voluntarily prohibit her nationals or vessels from carrying on pelagic fur sealing in the waters in question, and is moreover prepared to enter into negotiations toward the conclusion of a new convention."

Despite strong pressure from some sectors of the U.S. fishing industry, the United States government had managed not to include specific fishery articles in the draft peace treaty, except for Article 9 which set forth Japan's obligation to enter into negotiations with Allied Powers so desiring for the conclusion of bilateral and multilateral agreements on high seas fisheries. Negotiations for a tripartite fisheries convention between Canada, Japan, and the United States began on November 5, 1951, and were concluded on December 14. The Japanese delegation was shocked by the United States-Canada proposal for adoption of the abstention principle, which was an extreme form of resource allocation, not so much because Japan would have to refrain from fishing for North American salmon, halibut, and herring, but because of the potential effects of the adoption of such a principle on future fishery negotiations with other countries. Japan had no choice, however, and the treaty[14] was signed (on May 9, 1952) immediately after the entering into force of the peace treaty (April 28, 1952).[15] Except for those provided by the North Pacific fisheries convention, all restrictions on Japanese high seas fishing were removed.

[14] International Convention for the High Seas Fisheries of the North Pacific Ocean. The ratification of the treaty by Canada was delayed until 1953 due mainly to objections from the fishermen's union on the Pacific coast.

[15] Signed by 48 nations of the Allied Powers and Japan. Two separate peace treaties were signed, one with India and one with the Republic of China, both entering into force in 1952.

Implementation of the North Pacific Fisheries Convention

Since the establishment of the International North Pacific Fisheries Commission (INPFC) under the convention, two aspects of the implementation of the treaty provisions have been subject to intensive discussion between the representatives of the three governments: the possibility of moving the salmon abstention line (provisionally established at long 175°W) on the basis of scientific evidence and the question of whether the stocks on the abstention list continued to qualify for abstention. An enormous amount of research effort has gone into the study of the offshore distribution of all species of salmon, resulting in convincing evidence that a substantial portion of the North American salmon, particularly Bristol Bay sockeye salmon, enter the waters west of long 175°W and that, on the other hand, substantial numbers of Asian chum and pink salmon migrate into the waters east of long 175°W.[16] As the commission's recommendations have to be made unanimously, no action has been taken for moving the provisional line in either direction.

The convention provided that, during the initial 5-year period, no examination or recommendation be made as to whether the stocks continue to qualify for abstention. The period expired in 1958 and subsequent examinations of qualifications for abstention have resulted in some changes in the stocks on the abstention list. The following stocks have been removed from the list: the herring stocks off the coast of Alaska south of the Alaskan Peninsula and east of the meridian passing through the extremity of the Alaskan Peninsula; the herring stocks off the coast of the United States, south of the entrance to the Strait of Juan de Fuca; the herring stocks off the west coast of the Queen Charlotte Islands; and most important, the halibut stock of the eastern Bering Sea.[17]

[16] For the results of scientific investigations, see papers in Bulletins of the International North Pacific Fisheries Commission, for example, Margolis (1963), Kondo et al. (1965), Hartt (1966), Margolis et al. (1966), Neave, Ishida, and Murai (1967), Shepard, Hartt, and Yonemori (1968).

[17] While the removal of the herring stocks may have been partly to demonstrate the workability of treaty provisions, that of the Bering Sea halibut stock was an issue of practical importance to all parties.

The convention could be terminated by any one of the contracting parties serving 1-year notice after a period of 10 years, that is, June 1963. The Japanese government proposed negotiations for a new convention, which would eliminate the abstention principle, and such negotiations have been held several times since 1963, with no result. The United States and Canada would not consider abolishing the abstention principle. Japan, too, appears to have carried out negotiations more as a political gesture than a serious attempt to change the *status quo*.

The North Pacific Fisheries Commission has broadened its scope of operation to some extent by including serious discussions on the crab stocks in the eastern Bering Sea and the groundfish stocks in waters off the United States and Canada. In the earlier years, unofficial and temporary agreements were made as to the extent of Japanese fishing for groundfish in the Gulf of Alaska, as well as the way Japanese crab fishing is to be conducted in Bristol Bay. These aspects are now dealt with under separate bilateral, executive agreements between the two governments. The Commission has also been publishing results of research conducted by the national agencies of the three nations under its auspices, as well as fishery statistics on such stocks as salmon, halibut, herring, king crab, tanner crab, and groundfish.

In short, none of the parties have seriously considered abolishing arrangements under the treaty, particularly that for salmon. Both Canada and the United States seem to be satisfied that the treaty protects the North American salmon stocks just as well as any other international agreement that can realistically be conceived, while Japan appreciates the fact that, in years of large Bristol Bay sockeye salmon runs, a substantial quantity of North American salmon can be caught by Japanese fishermen. The only new problem faced by the commission is the entry of South Korean fishermen into salmon fishing in Bristol Bay—a development which might undermine the whole setup of the North Pacific fisheries convention. As South Korea is not a party to the convention, the commission has not been able to take any action except to

express its concern over the matter, and the issue has been handled mainly through direct negotiations between the United States and South Korea. The Japanese government has taken some action to prevent the involvement of Japanese companies in the Korean venture. The amount of salmon taken by the Koreans is still relatively small, perhaps in the order of several hundred metric tons in 1970, but if Korean fishing continues even at this rate it will seriously affect the stability of the salmon situation in the eastern North Pacific.

Japan-Soviet Salmon Controversy

Japan planned to send, in 1956, as many as 19 salmon motherships to the northwestern Pacific, including the Okhotsk Sea. The Soviet government issued, in February 1956, a unilateral declaration to restrict salmon fishing in waters west of long 170°E. There had been indications that the Soviet government might take some action to stop the phenomenal expansion of the Japanese high seas salmon fisheries.[18]

The Soviet declaration included: establishment, as an interim measure before the conclusion of an appropriate international treaty, of a salmon regulatory area covering the eastern Bering Sea, the northwestern Pacific and the Okhotsk Sea (Figure 7) to restrict salmon fishing (by both Soviet and foreign nationals) during the period of spawning migrations; establishment of a catch limit for 1956 at 50,000 metric tons; issuance, by the Soviet authorities, of licenses for fishing in the area; enforcement of regulations by the Soviet authorities; and the assurance that freedom of navigation in the area would not be affected. The action taken by the Soviet government was obviously related to negotiations for the normalization of diplomatic relations which had come to a deadlock just before the Soviet declaration on fishing.

[18] For example, at a meeting of the Economic Commission for Asia and the Far East (ECAFE) in 1955, the Soviet delegation pointed out that the salmon stocks in Kamchatka and other areas were in danger of being destroyed because of overfishing by Japan. Also, during negotiations for the normalization of diplomatic relations, which had been carried out in London, the Soviet representative stressed the need for restricting fishing for conservation of resources.

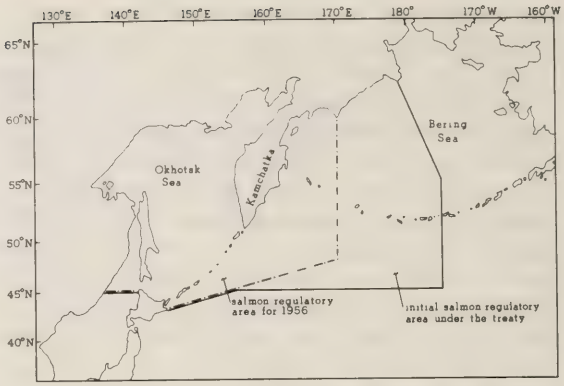

FIGURE 7.—Salmon regulatory area for the 1956 season and the initial salmon regulatory area under the 1956 treaty.

The Japanese government proposed immediate negotiations on fishery matters and sent to Moscow a team of top-notch experts headed by the Minister of Agriculture and Forestry. The convention, along with its protocol specifying regulatory measures and an agreement on emergency rescues, was signed on May 15. The treaty mentioned the maximum sustainable yield as the main objective, established the Japan-Soviet Fisheries Commission to consider joint conservation measures, set an annual salmon catch quota, and provided for enforcement of regulatory measures. The convention area was defined as the entire area of the northwest Pacific Ocean (excluding the territorial seas) including the Japan Sea, the Okhotsk Sea, and the Bering Sea. The protocol defined the regulatory area and spelled out regulatory measures to be taken for salmon, herring, and two species of king crab.

The convention provided that it would become effective upon entering into force of the peace treaty or the restoration of diplomatic relations. This undoubtedly speeded up peace negotiations, resulting in a joint declaration (to end the state of war and restore diplomatic relations) in December 1956. For all practical purposes, Japan's claim to the southernmost islands of the Kurile chain (which had been the main issue) was shelved. In order to permit Japanese salmon fishing for the 1956 season before the normalization of diplomatic relations, the two govern-

ments signed a temporary agreement which set a catch limit for that year. Japan undertook to reduce the size of the mothership fleet as a voluntary measure.

A lot of confusion occurred in connection with the procedure of obtaining licenses from the fishery inspection agency of the Soviet Ministry of Fisheries, but fishing did take place in the authorized areas in the Pacific and Okhotsk. Under the plan prepared before negotiations with the Soviet Union, 12 motherships with 375 catchers (including scouting boats) were to be sent to the northwestern Pacific and the western Aleutian waters, and 7 motherships with 213 catchers (including scouting boats) to the Okhotsk Sea. These were revised to 14 motherships with 447 catchers for the Pacific and Bering areas, and 2 motherships with 59 catchers for the Okhotsk Sea.

Since the regulatory area included part of the main fishing grounds of the land-based drift-net fishery, the total quota was divided into subquotas for the mothership fishery and the land-based fishery, each of which was further distributed among individual fishing vessels, establishing a precedent for an extremely detailed system of catch allocation. For the land-based drift-net fishery, quotas for individual vessels varied depending on their gross tonnage. The regulatory area under the temporary agreement did not cover vast areas to the east and south (Figure 7), and therefore a large amount (nearly one-half of the total take in 1956) was caught in waters outside. Due to delays in the issuance of licenses, the catch quota in the regulatory area was not filled within the established fishing period. The land-based longline salmon fishery, which began to develop in 1956, also took a considerable amount from waters outside the regulatory area.

The year 1957 was the first year of operation under the provisions of the convention. After hard negotiations both within and outside the fishery commission, the two governments settled for a total quota of 120,000 metric tons in the regulatory area, which now covered waters as far west as long 175°W but still excluded a substantial part of the land-based fishing grounds in the Pacific (see Figure 3 - Area A). The quota was divided, under Japanese regulations, between the mothership fishery and the land-based drift-net fishery and further among individual fishing vessels. The land-based drift-net fishery made more than one-half of their catch in outside waters, and the land-based longline fishery took twice the amount it caught in 1956, all from outside waters. The combined catch of all high seas salmon fisheries was about 162,000 metric tons as compared with the catch limit of 120,000 metric tons for the regulatory area. The 1958 agreement reduced the total quota to 110,000 metric tons which was again divided between the mothership fishery and the land-based drift-net fishery. Fishing in the Okhotsk Sea was further restricted, and a large closed area was established in waters off the east coast of Kamchatka.

Annual negotiations for salmon regulations have resulted in further restrictions on Japanese fishing. In 1959, the entire Okhotsk Sea was closed to high seas salmon fishing, and additional closed areas were established on the Pacific side. The catch quota for the regulatory area was further reduced to 85,000 metric tons, and a catch limit was set for sockeye salmon. In 1960, the Soviet Union proposed a southward expansion of the regulatory area to control fishing by land-based vessels carried out in outside waters. The Japanese undertook to take some domestic measures. The quota for the regulatory area has been reduced to 67,500 tons, with additional closed areas. A new step was taken in 1962 by designating the waters south of the previous regulatory area as Regulatory Area B, with the Japanese government undertaking to limit the catch in Area B to about 60,000 metric tons (with a 10% allowance). By then, the catch quota in the original regulatory area (now Area A) had been reduced to 55,000 tons. The Japanese government took a drastic measure to reduce the number of vessels both in the mothership fishery and the land-based drift-net fishery. Drift-net fishing in the Japan Sea was also reduced substantially. In 1964, the quotas were further reduced to 55,000 tons each for both Area A and Area B. Table 5 shows how the salmon catch

TABLE 5.—Japanese salmon catches by different fisheries compared with the total Soviet salmon catches. Catches are in metric tons $\times 10^3$.

Year	Japanese salmon catches					USSR total[1]
	Mothership	Land-based drift net	Land-based longline	Coastal traps and other fisheries	Total	
1956	93	41	8	9	151	160.0
1957	100	53	15	12	182	148.0
1958	92	74	16	14	196	71.0
1959	71	84	15	9	179	94.8
1960	54	67	17	9	147	71.0
1961	54	75	16	12	156	82.2
1962	45	42	15	15	116	61.8
1963	46	61	24	17	149	81.1
1964	44	45	12	16	117	46.9
1965	45	59	22	19	146	89.8
1966	39	50	21	16	127	59.7
1967	43	57	28	20	148	84.1
1968	38	51	13	12	114	39.2
1969	40	55	27	19	141	78.3

[1] Total of sockeye, pink, chum, coho, and chinook salmon.
Source of Japanese data: Ministry of Agriculture and Forestry (Japan) (1962-71).
Source of Soviet data: FAO Yearbook of Fishery Statistics and Kasahara (1963).

has been shared by different fisheries since 1956[10] (see Figure 3 for the fishing grounds of various fisheries). Although the details of changes in regulatory measures under the convention have not been mentioned, the above review clearly indicates that the Japanese high seas salmon fisheries have been subject to an increasing amount of control. The table also compares the Japanese catches (including small amounts of salmon destined for Japanese streams) with the Soviet catches.

Annual negotiations between the two governments both within and outside the commission have been very political, and in most cases important decisions have been made toward the end of each year's session as political compromises. From the data and information exchanged through the commission, it is difficult to evaluate the status of each of the important salmon stocks, particularly because the origin of much of the fish taken in offshore waters is not identifiable (except for such stocks as Karaginski pink salmon which to a large degree remain separate from others in their offshore distribution). The fact that the Japanese mothership fishery takes a large amount of Bristol Bay sockeye salmon in some years further complicates the situation.

The possibility of Korean fishermen conducting high seas salmon fishing in the Japan-Soviet treaty area has posed a problem which is substantially different from the question of Korean entry in the eastern Pacific. The Soviet Union has unofficially indicated that, if that happened, any amount of salmon Korea might take would have to be subtracted from the quota for the Japanese fisheries. Korean salmon fishing has not developed as yet, perhaps for two reasons: First, lacking diplomatic relations with the Soviet Union, their fishing vessels might be seized and fishermen jailed by the Soviet authorities if the Soviet government should take a strong stand, and there would be no way of settling the problem through negotiations, nor would any of the nations bordering the North Pacific take a sympathetic attitude toward South Korea. Second, the Japanese government and industry might take retaliatory measures such as more severe restrictions on sea food import from Korea.

[10] A 2-year cycle due to pink salmon fluctuations is obvious. This has been taken into account when setting quotas.

North Pacific Crab Controversies

International problems arising from king crab fishing after World War II are rather unique in several respects. Japan, the Soviet Union, and the United States have all been fishing for king crab, with Japan and the Soviet Union operating distant-water fisheries. While all three states fish for crab in the eastern Bering Sea, there has been no tripartite agreement dealing with crab fishing, international problems

being handled under three separate bilateral agreements, Japan-Soviet, United States-Japan, and United States-Soviet. Two of the three states, the Soviet Union and the United States, are parties to the 1958 continental shelf convention, which came into force in 1964, while Japan is not. The Soviet Union and Japan have developed a unique system to allocate tangle-net fishing grounds between their mothership fisheries both in Kamchatka and in the eastern Bering Sea.

As has been mentioned in the section on Review of Selected High Seas Fisheries, Japan planned to resume the mothership crab fishery during the 1952 season but did not proceed with the plan in fear of political repercussions from the United States. The fishery began in 1953 with one mothership jointly operated by the three biggest companies, each taking an equal share of interest and obligation, with a production quota of 50,000 cases (one case equals 48 cans of one-half pound each) set by the Japanese government, along with various restrictions on the fishing area and gear. This pattern of operation continued until 1956, when the production quota increased to 57,000 cases (plus some allowance). There were some U.S. crab vessels (trawlers) fishing in Bristol Bay from time to time, and arrangements were made for minimizing gear conflicts, but the U.S. catch was very small then. The rapid expansion of the Japanese crab fishery in Bristol Bay began in 1959, when the quota was raised to 70,000 cases. It was further increased to 80,000 cases in 1960, and in the same year a new mothership operation was authorized under an exploratory fishing license.[20] The Soviet crab fishery in Bristol Bay also started this year with one mothership. Thereafter expansion continued at an increasing rate.

By 1962, the fishery had grown to include three motherships in the spring season and two in the autumn. In 1963, the government consolidated the operations of different motherships and authorized only two, each managed jointly by several companies, with a total production quota of 235,000 cases (including frozen meat at a conversion rate of 100 tons of crab meat to 10,000 cases). The Soviet Union sent three motherships to the same area, resulting in some incidents of gear damage. During the period of expansion, the United States and Japan conducted research on the king crab stock in the eastern Bering Sea as part of the INPFC program, and the United States repeatedly expressed its concern over the condition of the stock.

In 1964, the United States enacted a law to prohibit exploitation of resources of its continental shelf by foreign nationals (the Convention on the Continental Shelf was ratified by the United States in 1961 and came into force in 1964). In a statement by the President, however, the United States indicated that due consideration would be given to the historical interest of Japan in king crab fishing in the eastern Bering Sea. Official negotiations were carried out during October-November 1964. As expected, Japan held the view that the king crab stock under question was a high seas resource, while the United States claimed the stock as a resource of the continental shelf over which the coastal state had exclusive jurisdiction. Although there was no agreement on the legal basis for regulating the exploitation of the stock, the two governments agreed to take certain measures for the seasons 1965 and 1966, including a reduction of the quota for the Japanese fisheries to 185,000 cases and various conservation measures applicable to the nationals of both nations. Fishing gear other than the tangle net and the pot was prohibited, and a large area was reserved exclusively for pot fishing.

A second round of negotiations was held in late 1966 and the agreement was extended, with the Japanese production quota further reduced to 163,000 cases for 1967-68. The agreement was revised again in 1968 for another 2 years, reducing the Japanese quota to 85,000 cases on the ground that the condition of the stock was deteriorating. For the first time, the need for paying attention to the condition of the tanner crab stock was discussed, and the Japanese government set a catch limit for tanner crab for the season 1969.

[20] The catch was processed to frozen crab meat, with a production quota of 180 tons. Fishing was conducted with three deck-loaded boats and one independent boat.

The U.S. government began negotiations with the Soviet Union for regulating crab fishing in the eastern Bering Sea. In this case, both governments were parties to the continental shelf convention and recognized the king crab stock as a resource of the U.S. continental shelf. An agreement was signed to limit the Soviet king crab production in the eastern Bering Sea to 118,600 cases for the seasons 1965 and 1966. The agreement has been revised from time to time since then, resulting in a continuous reduction of the Soviet quota, to 52,000 cases for 1969-70. The tanner crab catch was also limited to 40,000 cases per year for the same seasons.

The United States also suggested that there be a system of allocating tangle-net crab grounds between the Japanese and Soviet fleets, which would be similar to one implemented in Kamchatka for some time. Negotiations between the three governments were held in 1967, resulting in an arrangement shown in Figure 8. The agreement was renewed for 1969-70; the area reserved for pot fishing was expanded, and the remaining grounds for tangle-net were divided between the fleets of the two nations again. The allocated fishing strips have been rotated annually between the Soviet Union and Japan (there are many practical problems under this arrangement, including the use of fishing lots after the fleet of one nation has left).

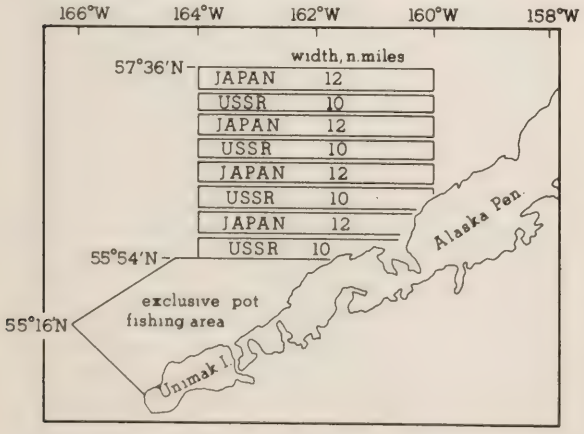

FIGURE 8.—Allocation of king crab fishing grounds in the eastern Bering Sea, 1969 (from Suisan-sha, 1970).

In short, a system of allocation has been developed between the three nations for crab fishing in the Bering Sea. Japanese fishing has been subject to catch limits under a United State-Japan agreement, which is legally not based on the continental shelf convention; Soviet fishing has been subject to catch limits under a Soviet-United States agreement which is based on the continental shelf convention; U.S. fishing has not been subject to catch limits; the Japanese and the Soviet quotas have been reduced, while the U.S. catch has increased rapidly in the last few years; a large area has been allocated exclusively for pot fishing; the tangle-net fishing area has been divided between the Japanese and Soviet fleets and rotated annually; size limits and other conservation measures have been applied to all nations. These arrangements have been made through executive agreements, and not by treaties requiring ratification.

On the Asian side, Japanese crab fishing in waters off the west coast of Kamchatka was resumed in 1956. The government authorized two motherships, each operated jointly by two companies, with a production quota of 60,000 cases each (plus 5% allowance), which was increased to 70,000 during the fishing season. Four motherships operated in 1956, with a production quota of 70,000 cases each (plus allowance). The actual production reached 313,000 cases.[21] The Japan-Soviet fishery convention, which entered into force in late 1956, included regulatory measures for two species of king crab (*P. camtschatica* and *P. platypus*), but the Japan-Soviet fisheries commission did not restrict fishing effort or the catch during the season 1957. At the annual meeting of the commission in 1958, the Soviet Union stressed the need to restrict crab fishing, and each government undertook to take certain measures (not as commission's decisions but as actions by each government), including a limitation on the number of motherships (no more than four Japanese motherships for 1958-60 and six Soviet motherships for 1958) and production quotas (no more than 320,000 cases per

[21] The government also authorized one mothership to operate in the Olyutorski area, but the fleet could not reach its production quota. The unfilled portion of the quota was taken by one of the four motherships operating in west Kamchatka.

year by Japan for 1958-60 and 480,000 cases by the Soviet Union for 1958). The commission recommended to close waters south of lat 53°N, and the Soviet government undertook to take a similar measure for fishing within its territorial sea. The national quotas for mothership fisheries were further reduced in 1959 to 280,000 cases for Japan and 420,000 cases for the Soviet Union. Various other measures also took effect to restrict fishing and avoid conflicts. Further changes were made thereafter to increase the proportion of the Soviet share in the total mothership catch and to reallocate fishing grounds between the fleets of the two nations (Figure 9), with the Soviet Union taking somewhat wider strips.

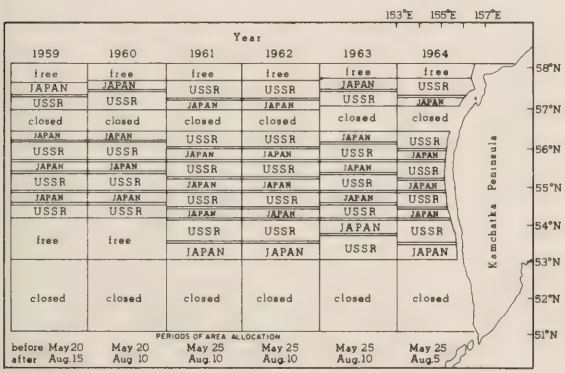

FIGURE 9.—Allocation of king crab fishing grounds off west Kamchatka, 1957-64 (from Norin Keizai Kenkyusho, 1965).

A new situation developed in 1968 when the Soviet government declared sovereign rights to the resources of the continental shelf and wished to enter into negotiations in 1969 for a separate agreement for crab fishing. As in the case of United States-Japan negotiations, Japan refused to recognize the Soviet claim not only on the ground that Japan was not a party to the continental shelf convention (the Soviet ratified the continental shelf convention in 1960) but also for the reason that she did not consider the crab a continental shelf resource. The fact that Japan is not a party to the convention might not have been considered a strong enough reason for arguing against the Soviet claim since the convention had been ratified by most of the major fishing nations. After prolonged negotiations, an agreement (in the form of an exchange of letters, along with a protocol and agreed minutes) was reached by shelving the positions of the two governments on legal questions.

Thus, the numbers of vessels (motherships or land-based vessels) were limited and the catch quotas (in terms of either canned crab produced or the number of crabs caught) established for *P. camtschatica* in west Kamchatka; "ibara crab" (a deepwater crab, *Lithodes aequispina*) in west Kamchatka; tanner crab in the western Bering Sea (off the Gulf of Anadyr and waters between Cape Olyutorskiy and Cape Govena); tanner crab, *P. camtschatica,* and *P. platypus* ("abura crab") in waters off the east coast of Sakhalin; hair crab (*Erimacrus*) and *P. brevipes* ("hanasaki crab") in waters around the southernmost islands of the Kurile chain (Figure 10).[22] Fishing grounds for all these fisheries were specified, and closed seasons, size limits, and various other restrictions applied. The Japanese government issued a new set of domestic regulations to cover these fisheries. Quotas for most areas were further reduced in 1970.

Fur Seal Convention

As mentioned above, Japan undertook, during the occupation period, to voluntarily prohibit her nationals or vessels from carrying on pelagic fur sealing, pending the conclusion of a new convention. Negotiations for a new convention took a number of years, and the convention signed in 1957 (came into force the same year) was called an Interim Convention for the Conservation of North Pacific Fur Seals. Although it is

[22] Japan had developed a substantial mothership fishery for *P. platypus* in waters along the coast of Olyutorskiy. This fishery was terminated by the 1969 crab agreement on the ground that the stock had been depleted. The remaining part of the crab fishery in that region was mainly for tanner crab in waters east of Cape Navarin and west of Cape Olyutorskiy conducted by motherships and land-based vessels. Japanese tanner crab fishing in waters off the west coast of Sakhalin and Primore (the Soviet mainland coast of the Japan Sea) was also terminated with the fishing vessels transferred to the tanner crab grounds along the east coast of Sakhalin.

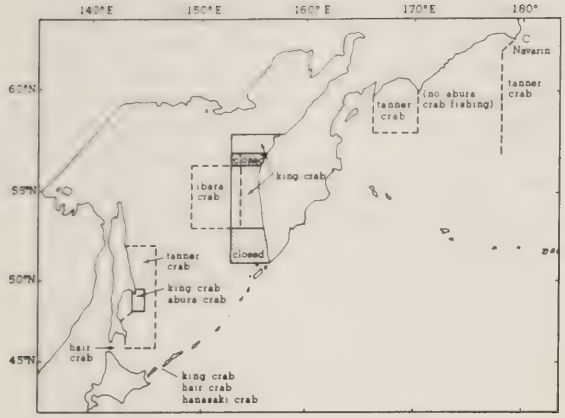

FIGURE 10.—Crab fishing regulated under the Japan-USSR crab agreement, 1969 (from Suisan-sha, 1970).

still called an interim convention, it is almost a permanent arrangement. Pelagic sealing is prohibited; a system of product distribution more or less similar to that under the 1911 convention is in effect. While the previous convention carried out its tasks without forming an international body, the new one established an international commission. Much emphasis has been placed on a research program to arrive at an optimum level of harvesting and examine the effects of seal predation on other fishery resources.

Rhee Line

Perhaps the most difficult fishery controversy Japan has ever faced is the Rhee Line issue arising from a declaration by President Syngman Rhee of the Republic of Korea concerning marine sovereignty. Korea had ceased to be a Japanese colony at the end of the war, and negotiations for normalizing relations between the Republic of Korea (South Korea) and Japan began in February 1952 and continued until June 1965, for a period of 13 years. The most difficult of all the problems was the fishery dispute. The seizure of Japanese fishing vessels by Korean authorities for alleged violation of waters under Korean jurisdiction started as early as 1947, immediately after the postwar expansion of Japanese fisheries began, and incidents increased greatly in the following few years. On January 18, 1952, President Syngman Rhee issued a declaration claiming sovereign rights to all natural resources over a vast area delimited by the so-called Rhee Line (Figure 11).[23] On September 8, 1953, the Korean government further issued a statement ordering all Japanese fishing vessels to stay outside the line, and enforced the order strictly at the height of the Japanese mack-

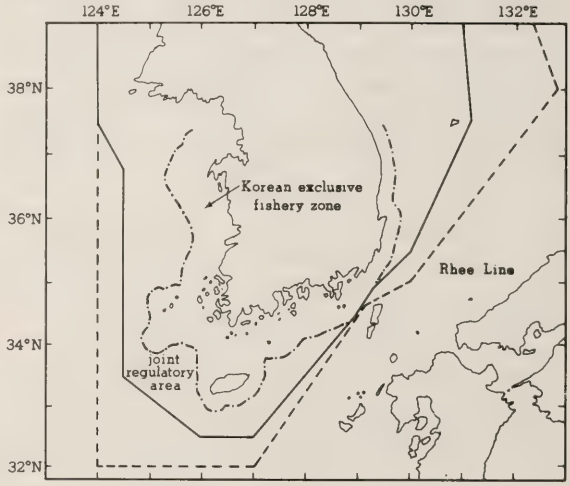

FIGURE 11.—Korean exclusive fishery zone and the joint regulatory area under the Japan-Korea fishery agreement (from Fishery Agency, 1965). Large portions of the joint regulatory area are closed to trawl fishing.

erel fishing season. Four major Japanese fisheries were affected: the pole-and-line mackerel fishery (with lights), the purse-seine fishery for jack mackerel, the trawl fishery west of long 130°E, and, least important, the trawl fishery east of long 130°E. Between 1947 and 1959, 326 Japanese fishing vessels were seized and the bulk of the 3,900 fishermen involved were jailed (of these, 141 vessels and practically all fishermen were returned later). The Japanese government did not contest the Korean claim by force but merely tried to minimize the number of incidents by running her patrol boats along the Rhee Line.

[23] The preamble of the declaration referred to established international precedents, and the Truman proclamations of 1945 were mentioned in this connection.

Among the issues taken up during negotiations for the normalization of diplomatic relations, the treatment of property claims and the conclusion of a fishery agreement were most difficult, and the fishery dispute perhaps created far more problems than the claim issue, for it affected the operations of thousands of Japanese vessels. (Among the other main agenda items were the establishment of basic relations between Japan and the Republic of Korea, the laying of submarine cables, and the conclusion of a treaty concerning trade and navigation.) The final settlement reached in June 1965 included four agreements, of which one on property claims and economic cooperation and one on fisheries were the most important from a practical point of view. The former specified the forms and amounts of monetary compensations. Japan undertook to provide $300 million (360 yen per dollar) as grants, $200 million as government loans (at 3.5% with a repayment period of 20 years including 7 years of grace),[24] and more than $300 million of commercial credit at a low interest rate. A substantial portion of the total sum was expected to be spent for fishery development, mainly in the form of vessels and equipment.[25]

The agreement between Japan and the Republic of Korea concerning fisheries consisted of the mutual recognition of a right to establish a 12-mile fishery zone over which the respective coastal state would have exclusive fishery jurisdiction, and the establishment of a joint regulatory area in which fishing by the nationals of both nations was to be restricted as to the numbers, sizes, and types of fishing vessels as well as the annual catches of the fisheries concerned. Closed areas, closed seasons, and other restrictions were also applied. The Korean exclusive fishery jurisdiction zone and the joint regulatory area established under the agreement are shown in Figure 11. Japan established a 12-mile fishery zone along the coast facing Korea. Arrangements under the agreement, its protocol, and subsequent agreements are extremely complex.

The effects of the fishery agreement have been quite remarkable. Disputes over fishing activities have ended almost completely.[26] No major controversies have developed from the annual meetings of the Japan-Korea fisheries commission established under the agreement. During the period of negotiations, the Korean fishing industry had grown to a strong competitive industry which no longer needs much legal protection against Japanese fishing activities. It is obvious that, on a give-and-take basis, Korea gained much more than she gave up in the overall settlement, which to a large extent depended on the resolution of fishery disputes. The fishery agreement and its protocol also indicate how far the Japanese government might go in making complicated arrangements to settle international fishery problems.

Conflicts with People's Republic of China

After the outbreak of the Korean War, Japan began to have serious problems with the People's Republic of China.[27] During 1951-54, more than 150 vessels, practically all pair trawlers, were seized in the East China Sea by the Chinese patrol vessels (Norin Keizai Kenkyusho, 1965). Negotiations began in 1954 between a Japanese nongovernmental organization and a Chinese fishery association, resulting in a 1-year agreement on the operation of the trawl fishery in the East China Sea (including the Yellow Sea). The coastal areas were closed to trawl fishing, and the numbers of Japanese and Chinese trawl vessels to operate in certain areas during certain periods were limited. The agreement was extended for another 2 years but was terminated by China in 1958, resulting in another outbreak of incidents. A separate agreement was made in 1959 concerning emergency port calls by

[24] Loans may be used for both capital goods and material.

[25] The Korean government originally envisaged investing roughly $150 million in fishery development, but actual items to be provided by Japan have been negotiated annually.

[26] Most of the fishery problems since the conclusion of the treaty agreement have been in connection with the export of Korean fishery products to Japan, particularly dry laver, the only export market of which is Japan who also has a very large laver aquaculture industry.

[27] Although Japan was not involved in the war, she provided bases close to Korea and was also an important source of war supplies.

fishing vessels (each side designated three ports for emergency calls). Negotiations for another fishery agreement began in 1963, and the previous agreement was revived with certain modifications for another 2 years. The agreement has since been revised and modified from time to time. Under the agreement signed in June 1970, the Japanese delegation agreed to enter into negotiations with a view to restricting purse-seine fishing. A new agreement was signed in December 1970 establishing three regulatory areas for purse seining: one is closed and the numbers of Japanese and Chinese seiners are limited in the remaining two.

Although these agreements have helped reduce the number of incidents greatly, their nongovernmental status made it difficult for Japan to enforce the agreed regulatory measures, and many violations have occurred. The important stocks of groundfish in the East China Sea are generally in poor condition due to overexploitation. There is no way of developing an overall international agreement to protect and allocate these resources, for diplomatic relations do not exist among some of the countries exploiting the same stocks. China has taken the greatest proportion of the total landings, although no reliable estimate is available. Japan's catch has been substantial, while the proportions taken by South Korea, North Korea, and Taiwan have been relatively small.

Extension of Limits of National Jurisdiction

Japan has been dealing with an increasing number of problems arising from the extension of the limits of national jurisdiction through unilateral claims by coastal states. As a general trend is for more nations to claim broader zones, a review of Japan's responses to these claims is appropriate.

United States.—Except for the abstention provisions of the North Pacific fisheries treaty, the Japan-United States crab agreement, and regulatory measures recommended by INPFC for Bering Sea halibut, Japanese fisheries in the eastern half of the Pacific Ocean have been relatively free of restrictions. The Japanese government initially controlled the expansion of groundfish fishing into waters south of the Alaskan Peninsula on the basis of unofficial discussions with the United States, but the situation changed in 1965 when the government issued regular licenses to a substantial number of vessels.

Negotiations for resolving problems arising from the establishment of an exclusive fishery jurisdiction zone by the United States in 1966 (3-12 miles) began in January 1967, and an agreement came into effect in May 1967. While the United States took the position that an exclusive fishery zone could be established by a domestic law, Japan held the view that such a zone had no legal basis without an international agreement. As in the case of the crab dispute, the governments shelved their legal positions and worked out practical arrangements.

The agreement covered a wide variety of fishing activities, both within and outside the fishery zone. For example, Japan was permitted to continue the established fisheries within the fishery zone for crabs off the Pribilof Islands, groundfish along the Aleutians except during certain periods in certain areas, whales along the Aleutians and the Gulf of Alaska except between long 150°W and 163°W, salmon off the Aleutian Islands west of long 175°W, and tunas except in waters around the Hawaiian Islands and off the mainland coast. Certain areas within the zone were also designated for loading and support activities. In turn, Japan undertook to refrain from fishing in certain areas of international waters during the first part of the halibut season and during the main crab pot fishing season. The agreement has since been revised twice, the most recent revision (effective January 1971) being summarized in Figures 12 and 13. (In comparison, the United States-Soviet agreement is summarized in Figures 14 and 15.)

It is obvious that the United States has tried, with some success, to reduce the effects of foreign fishing in international waters on important domestic fisheries in turn for allowing foreign fishermen to continue their fishing in areas within the exclusive fishery zone where such fishing does not seriously affect domestic fisheries. The United States has also avoided con-

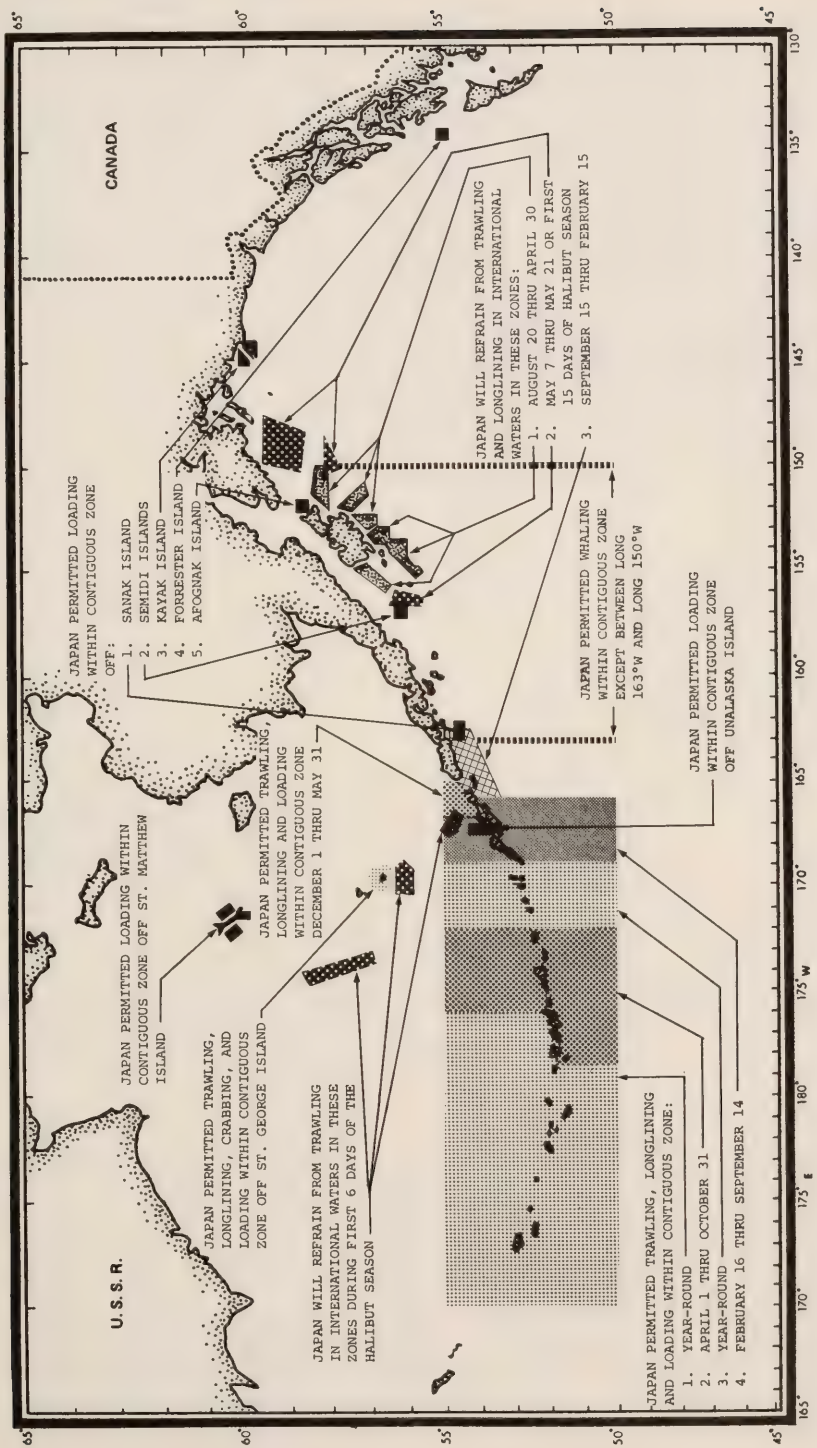

FIGURE 12.—Arrangements under the United States-Japan fishery agreement (December 1970) concerning the U.S. contiguous fishery zone, off Alaska (taken from Commercial Fisheries Review, 1971a).

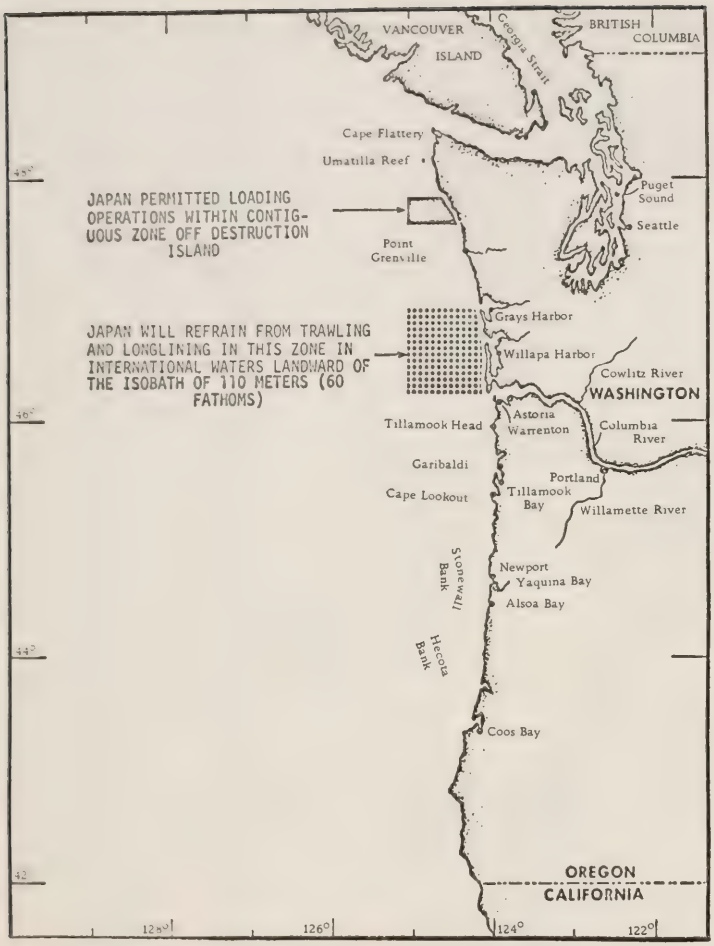

FIGURE 13.—Arrangements under the United States-Japan fisheries agreement (December 1970), off the Pacific Northwest (taken from Commercial Fisheries Review, 1971a).

cluding a long-term agreement which might affect her position with respect to global negotiations now being held.

Mexico.—When Mexico declared, in 1967, a 3-mile exclusive fishery zone beyond her 9-mile territorial sea, Japan entered into negotiations with Mexico to protect her vested interest in tuna longline fishing in waters between 9 and 12 miles. There was no agreement on the legality of the Mexican claim, but practical arrangements were worked out so that, except in areas particularly important to sport fishing, Japan was able to continue longline fishing in waters between 9 and 12 miles without exceeding the amount of effort in the previous years. The agreement was in the form of an international treaty effective over a period of 5 years. This was a relatively minor dispute.

New Zealand.—New Zealand declared a 9-mile exclusive fishery zone beyond her 3-mile territorial sea in 1966. Japan entered into negotiations with New Zealand to protect her longline porgy ("tai") fishery within the newly claimed area. The agreement reached in 1967 allowed Japanese fishing to continue in waters between 6 and 12 miles without increasing the number of vessels, nor their size, until the end of 1970 (for 5 years after the establishment of the exclusive

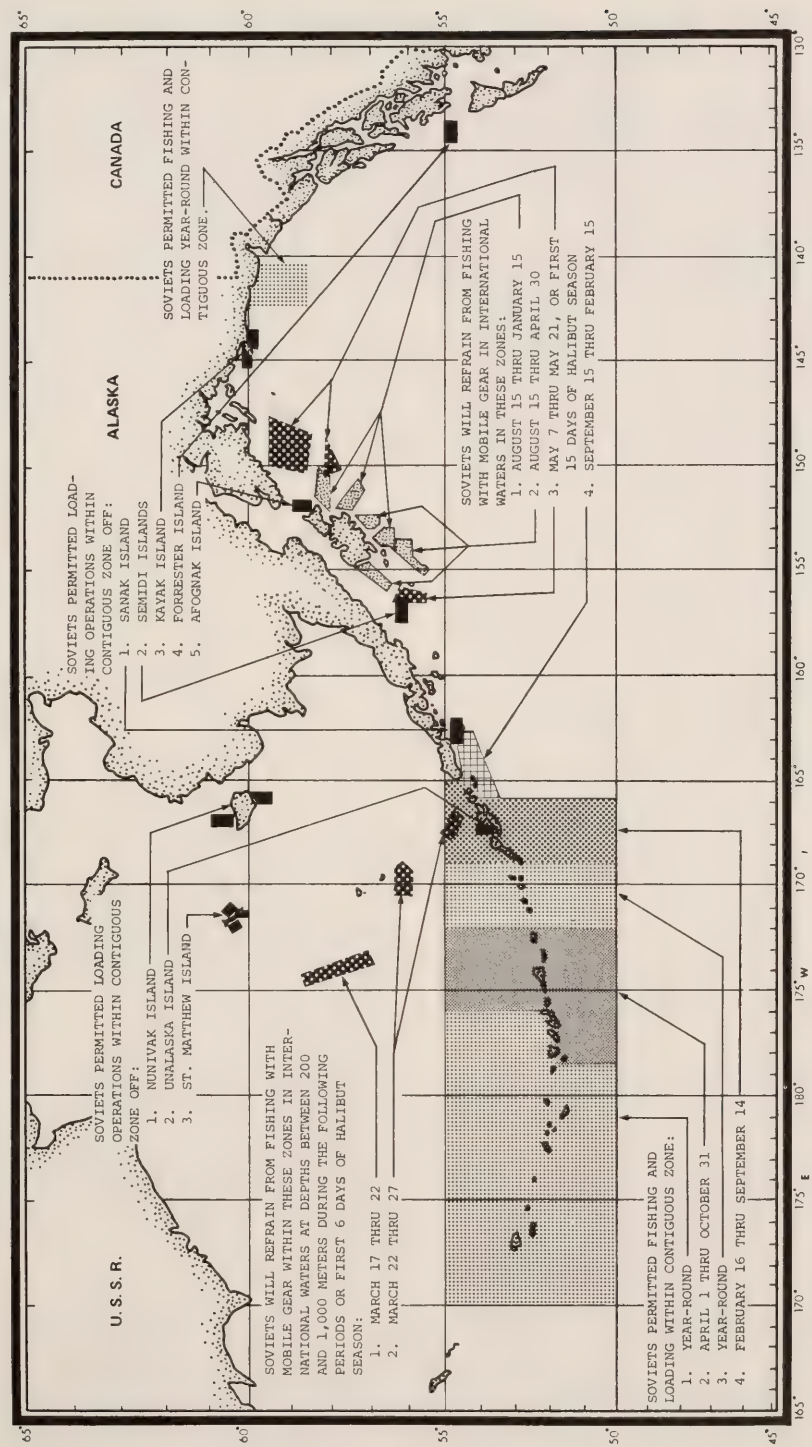

FIGURE 14.—Arrangements under the United States-USSR fisheries agreement (February 1971), off Alaska (taken from Commercial Fisheries Review, 1971b).

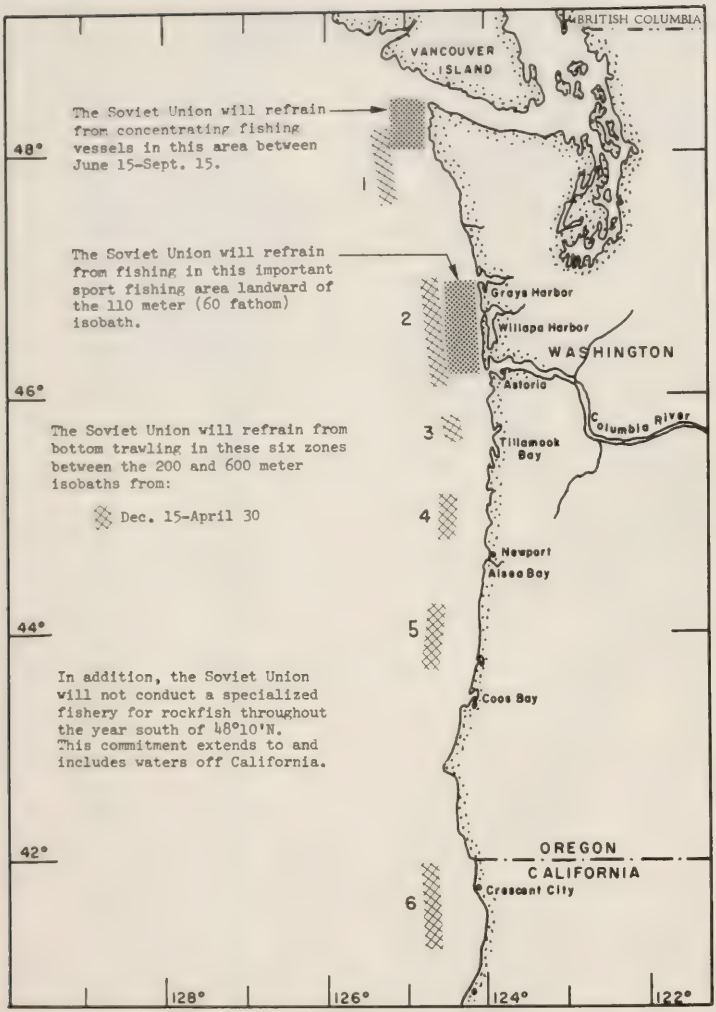

FIGURE 15.—Arrangements under the United States-USSR fisheries agreement (February 1971), off the Pacific Northwest (taken from Comemrcial Fisheries Review, 1971b).

fishery zone in January 1966). Japanese fishing within the zone terminated at the end of this period.

Australia.—Australia declared, in 1968, a 9-mile exclusive fishery zone beyond her 3-mile territorial sea (including Territory of Papua), and at the same time indicated that Australian ports would in principle be closed to foreign fishing vessels. The Japanese tuna longline fishery, mainly for southern bluefin, would be affected, especially by the closure of ports. Tuna vessels would have to pay license fees to fish in the exclusive fishery zone. Negotiations took over 3 months. As usual, the question of legality of the claim was shelved, but the agreement reached envisaged the phasing out of Japanese fishing in 7 years. Australia designated four ports for Japanese tuna vessels to visit, each paying a small fee.

Indonesia.—In 1957, Indonesia claimed all waters within her archipelago as internal waters and started seizing Japanese tuna boats, particularly in the Banda Sea, which was an important tuna fishing area for smaller longliners. An

agreement was concluded, in 1968, between the Japanese industry (represented by the Federation of Japan Tuna Fishery Co-operatives and the National Federation of Fishery Co-operatives) and the Indonesian Ministry of Agriculture. The number of vessels to operate in the Banda and Ceram Seas was limited for each of the three size categories (most of the vessels being less than 70 gross tons) with a maximum total number of 250 vessels and an annual quota of 15,000 metric tons. Each vessel was to pay a sum of money for using Ambon as a supply base. A substantial amount of technical assistance was also to be provided by Japan in connection with the agreement. The agreement was for a period of 1 year, but has been renewed every year with minor changes.

West Africa.—The Japanese trawl fishery along the coast of West Africa has been facing increasing difficulties due to the extension of the territorial sea and other unilateral claims by the coastal states (see Table 6 for present status). Fishing in the northern area, along the coast of Spanish Sahara and Mauritania for cuttlefish, octopus, and porgies, has been affected seriously by the estabishment of an exclusive fishery zone (6-12 miles) by Spain and the extension of the territorial sea by Mauritania. In the case of Mauritania, an extensive straight base line measuring some 90 nautical miles was used along the northern part of its coast. Both governments enforced these measures and seized some Japanese vessels.

TABLE 6.—Territorial seas and exclusive fishing zones claimed by West African countries as of April 1971. Distances are in nautical miles and year of enactment is in parentheses.

Countries	Territorial sea	Outer limit of exclusive fishing zone
Morocco		12 (1967)
Spanish territories	6 (1957)	12 (1967)
Mauritania	12 (1967)	
Senegal	12 (1967)	18 (1968)
Gambia	12 (1969)	
Portuguese territories		12 (1966)
Guinea	130 (1964)	
Sierra Leone	12 (1965)	
Liberia	12	
Ivory Coast	6 (1967)	12 (1967)
Ghana	12 (1963)	[1]
Togo	12 (1964)	
Dahomey	12 (1965)	
Nigeria	12 (1967)	
Gabon	25 (1970)	
Congo (Brazzaville)	12 (1969)	
Congo (Kinshasa)	No legislation	
South Africa	6 (1963)	12 (1963)

[1] A 100-mile conservation zone (1963).
Source: FAO (1971).

While Spain has not agreed to negotiate with Japan on fishery problems arising from her action, Mauritania did. After a long period of negotiation, a 1-year agreement was signed in February 1970 (came into effect in April 1970) which might be extended for another year with the consent of both parties. It provided for 24 Japanese trawlers to operate within the 12-mile zone, plus 5 small vessels within 3 miles of the coast. The latter vessels would deliver their entire catch to Mauritania, which would then be sold to Japan. Each of the 24 trawlers would provide training for three Mauritanian fishermen, and each of the five small vessels for one fisherman. Japan also undertook to purchase fish taken by local Mauritanian fishermen. Although Japan would pay a certain sum (approximately $28 per gross ton of each vessel per year), Japan did not want to have it called "a fishing fee." As far as Japan was concerned, the money would be paid as a form of aid or economic cooperation in exchange for permission for Japanese vessels to fish within the zone and to use Mauritanian port facilities. The Japanese delegation for negotiation was composed mainly of industry representatives.[28]

Participation in International Fishery Conventions

Japan has recently joined four multilateral fishery conventions: the Northwest Atlantic fisheries convention (joined 1970), the Inter-American tropical tuna convention (joined 1970), the Atlantic tuna convention (came into force 1969), and the Southeast Atlantic fisheries convention (came into force 1971). Thus, Japan is now a member of the following fisheries commissions established under international conventions: the International Whaling Commis-

[28] The legal status of this agreement is not clear to the author. Mauritania has also concluded bilateral fishery agreements with such other nations as Greece, Italy, Spain, and the Netherlands.

sion, the North Pacific Fur Seal Commission, the International North Pacific Fisheries Commission, Japan-Soviet Fisheries Commission, the Japan-Republic of Korea Joint Fisheries Commission, the International Commission for the Northwest Atlantic Fisheries, the Inter-American Tropical Tuna Commission, the International Commission for the Conservation of Atlantic Tunas, and the International Commission for the Southeast Atlantic Fisheries now in the process of being established. As mentioned, above, Japan is a party to a large number of bilateral agreements, including some nongovernmental arrangements, with a variety of nations. Consultations have also been taking place annually between the tuna industries of the three major longline fishing nations: Japan, Taiwan, and South Korea.

FORMS OF INTERNATIONAL ARRANGEMENTS AND MEANS TO IMPLEMENT THEM

Forms of Arrangements

The official position of the Japanese government concerning high seas fishing has always been for the basic freedom of fishing and, where conservation measures are required, free competition between nations within the limitations equally applicable to all. She has always supported a narrow territorial limit; she is still not a party to the 1958 continental shelf convention, nor the 1958 convention on fishing and conservation of living resources. In practice, however, she has accepted various forms of allocation as means to accommodate the conflicting interests of the nations concerned, although she has seldom taken the initiative for making such arrangements.

The most extreme form of resource allocation is, of course, "abstention," which Japan accepted, though under unusual circumstance. In most other cases, the allocation of resources has been implemented through a combination of catch quotas, often with a system of allocating fishing grounds, and direct control on fishing effort. This applies to all salmon and crab fisheries (and now herring fishing) under the Japan-Soviet fishery agreements, the crab fishery under the Japan-United States agreement, the fisheries regulated under the Japan-Korea fishery treaty, whaling in the Antarctic as well as in the North Pacific, and many other cases. The principle of product distribution is also practiced under the fur seal treaty. In most cases, a total quota is applied to fishing in a specific high seas area and/or for a specific resource. To control fishing effort, the types and numbers of vessels allowed to operate in the area are restricted. The total quota is usually divided between operating units, such as mothership fleets or independent vessels. The available fishing grounds, too, are often allocated between different sectors of the fishery. Such usual measures as closed seasons, closed areas, size limits, gear restrictions, etc. are applied. In the case of king crab, the international tangle-net fishing grounds are divided into a number of small fishing lots which are allocated and regularly exchanged between the Soviet and Japanese fleets (see Figures 8 and 9).

Japanese responses to what she considers unilateral actions have also been rather pragmatic. For example, Japan is not a party to the continental shelf convention, while the United States and the Soviet Union are. Yet, arrangements made under the Japan-United States crab agreement and United States-Soviet crab agreement are in principle the same. Japan claims a 3-mile territorial limit, while the Soviet Union claims a 12-mile limit. But Japan has never attempted to fish within 12 miles of the Soviet coast, except around the southernmost islands of the Kurile chain. The treatment of problems arising from the establishment of an exclusive fishery zone by the United States is not substantially different between the United States-Japan fishing agreement and the United States-Soviet fishing agreement (see Figures 12-15). On a global basis, different arrangements have been made to resolve fishery problems arising from the establishment of an exclusive fishery zone. The United States-Japan fishing agreement mentioned above is on a give-and-take basis. Under the Japan-Mexico fishing agreement, Japan managed to continue tuna fishing in much of the waters concerned. In both the Japan-Australia agreement and the Japan-New Zealand agree-

ment, Japan agreed to phase out her fishing activities in the respective zones within a relatively short period of time (5 years for New Zealand and 7 years for Australia). Different forms of compensation and payment have been used, e.g., the Japan-Korea agreement, the Japan-Indonesia agreement, and the Japan-Mauritania agreement, sometimes on a large scale. Political trade offs are not unusual either. Japanese pragmatism has gone to the extent of concluding nongovernmental agreements to settle fishery problems, as seen in negotiations with the People's Republic of China and Indonesia.

In the entire history of international fisheries disputes after World War II, Japan has never contested unilateral jurisdictional claims by force. Even at the height of the Japan-Korea dispute, when a large number of Japanese vessels were being captured by Korean patrol boats, Japanese patrol boats never opened fire or tried to recapture the vessels by other means. Japan has not challenged the 200-mile territorial sea or fishing limit claimed by Latin American nations except by protests through diplomatic channels. In short, despite her rigid position regarding the freedom of fishing and limits of national jurisdiction, Japan has in practice accepted various forms of allocation, including the allocation of resources, division of catch, allocation of fishing grounds, as well as a system of revenue sharing in exchange for giving up the right to exploit a resource on the high seas (fur seal). She has done so in most cases reluctantly and after long, hard negotiations.

Means to Control Fisheries to Meet International Problems

Japan has so far found some way of settling almost every major international fishery dispute, as well as extremely complicated problems of domestic fisheries, some of which were mentioned in connection with the development of trawl fisheries in Japan. This is not an easy task, if one considers the diversity of fishing and processing activities and the enormous amount of investment in every sector of the industry. What has made it possible for the Japanese government to cope with all these conflicts from various sources is the existence of an effective, centralized system of control as briefly described in the introduction of this paper. The so-called licensing system applies to practically all offshore fisheries. Although legal authority is vested in the Minister of Agriculture and Forestry, the Fishery Agency, which is subordinate to the Ministry, has in fact full power to control all major fisheries. Thus, the central government may, and does in practically all cases, restrict the type, number, and often size of the vessels allowed to operate in a given area and/or for a given resource. Although objectives are different from case to case and change from time to time, the basic concept is to give the central government a strong means to allocate resources among different sectors of the industry to accommodate their conflicting interests. The administration of fisheries under this system is naturally subject to pressures from different groups, including large fishing companies, vessel-owner associations, and fishermen's associations, but institutional changes are made only through this centrally controlled system. The system is also used, in most cases rather effectively, to accommodate such changes as the government and industry consider necessary for meeting new international developments or resolving international fishery issues. It is, of course, debatable whether this system has in the long run facilitated the rational development of the Japanese industry, for there is no way of telling how the industry would have developed under any other system. Japan can not go back to 1946 and start developing fisheries again.

Another important factor which has contributed toward facilitating international fishery arrangements is the existence of well-organized associations representing various segments of the industry. As briefly described by Kasahara (1964), the structure of the Japanese fishing industry is one of extreme complexity. There still exist a huge number of small fishing craft, including many nonpowered vessels, while large companies operate gigantic motherships and factoryships. Between these two extremes, there are vast numbers of vessels of all kinds and sizes. The existence of the large fishing companies running most of the important distant-water fisheries deserves special attention. The following

brief description of the biggest four indicates the magnitude of large company operations (data are mostly for 1968 and do not include their subsidiary companies):

Taiyo Gyogyo Company, Ltd.

In addition to fishing, fish processing, and marketing, engaged in a wide variety of other activities.

Gross sales	$472 million.
Number of employees	10,890 including 6,880 aboard ships.
Number of vessels	486, with a combined gross tonnage of 225,000.
Major fishing activities	Whaling, the mothership salmon fishery, the mothership trawl fishery, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific) and the East China Sea, overseas shrimp ventures, and others.

Nippon Suisan Company Ltd.

In addition to fishing and fish processing, a substantial interest in transport business, with four large vessels carrying oil and ore.

Gross sales	$195 million.
Number of employees	7,950 including 3,960 aboard ships.
Number of vessels	131, with a combined gross tonnage of 396,000.
Major fishing activities	Whaling, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific) and the East China Sea, the mothership trawl fishery, the mothership salmon fishery, the mothership crab fishery, overseas shrimp ventures, and others.

Nichiro Gyogyo Company, Ltd.

Before the war, the company monopolized Japanese salmon fishing from the Russian territory. Now engaged in diversified activities.

Gross sales	$155 million.
Number of employees	5,800 including 3,190 aboard ships.
Number of vessels	113, with a combined gross tonnage of 98,000.
Major fishing activities	The mothership salmon fishery, the mothership crab fishery, the mothership trawl fishery, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific), overseas shrimp ventures, tuna fisheries, and others.

Kyokuyo Hogei Company, Ltd.

Started as a whaling company but has since diversified its activities.

Gross sales	$85 million.
Number of employees	3,640 including 1,810 aboard ships.
Number of vessels	48, with a combined gross tonnage of 100,000.
Major fishing activities	Whaling, the mothership salmon fishery, trawl fisheries in distant waters (including the Bering Sea and northeast Pacific), overseas shrimp ventures, the tuna longline fishery, crab fishing, and others.

Among these four companies, they own practically the entire whaling business excepting minor operations by two small companies, 8 out of 11 salmon motherships,[29] roughly two-thirds of the crab fisheries in the eastern Bering Sea, three-quarters of the mothership crab fishery in west Kamchatka, some 80% of the Bering Sea mothership trawl fishery, most of the large stern trawlers operating in the North Pacific, West Africa, and other distant waters, as well as much of the shrimp ventures abroad. It means that the government can handle the industry aspects of most of the international problems concerning these fisheries by communicating with these and a few other companies (some of them subsidiaries of the big ones). The government sometimes has forced them to conduct joint operations. Thus, one of the two mothership crab fleets fishing in the eastern Bering Sea is managed jointly by four companies, the other by five companies. Representatives of these companies, particularly the first three, often participate in international negotiations.

The structure of fishery trade associations in Japan is rather complicated. The following is a brief description of some of the associations concerned with international aspects of Japanese fisheries:

[29] Salmon catcher boats are largely owned by small companies and individual vessel owners.

Japan Fishery Association (*Daisui*) generally represents the interest of larger fishing companies engaged in offshore and distant-water fisheries. It is often represented in important international fishery negotiations. It develops industry policies on international fishery problems and also deals with specific disputes. It also arranges for long-term, low-interest loans for the development of distant-water fisheries. The present chairman of the association is one of the most experienced Japanese in international fishery negotiations.

National Federation of Fishery Co-operatives (*Zengyoren*) provides nationwide representation for Japanese fishery co-operatives. Two of the main areas of activity are the procurement and distribution of duty-free diesel oil and fish marketing, but the federation is involved in international fishery negotiations from time to time.

Federation of Japan Tuna Fishery Co-operatives (*Nikkatsuren*) is the most powerful association for Japanese tuna fisheries, participated in by tuna and skipjack vessel owners through their local cooperatives,[30] and is involved in most of the international negotiations concerning tuna fisheries. Together with Zengyoren, the federation signed the Banda Sea agreement with Indonesia. The federation is making an effort to restrengthen the Japanese tuna longline fishery with substantial success. It buys in when the market is weak. It has been campaigning for increased domestic consumption of the tuna species that have been mainly exported, resulting in an appreciable increase in the consumption of canned albacore tuna. It has promoted consultations with the tuna industries of South Korea and Taiwan. It plans to institute voluntary restrictions, mainly closed seasons, on fishing for southern bluefin tuna (in effect as of October 1971). It compiles the most complete statistics of the longline fishery available in Japan.

[30] Tuna operators not eligible to cooperative membership under the Japanese fishery cooperative law, mainly companies operating large tuna boats, are organized under the Japan Tuna Fishery Association (Nikkatsukyokai). Nikkatsuren and Nikkatuskyokai always work together.

Federation of Japan Salmon Fishery Co-operatives (*Nikkeiren*) represents salmon catcher boat owners and is mainly concerned with catch quotas for the mothership salmon fishery and negotiations with mothership owners for profit sharing (formerly for selling prices). There are also associations representing such other salmon fisheries as the land-based drift-net fishery and the land-based longline fishery.

National Federation of Medium Trawlers represents bottom trawl fisheries in waters east of long 130°E, including the category called "Hokutensen" (see page 233). As the importance of "Hokutensen" increases, the association is now concerned about the condition of the pollack stocks in the northern areas (Kamchatka, North Kuriles, and Bering Sea) on which the entire fishery is based.

Japan Trawler Fishery Association represents trawl fisheries (largely by pair trawlers) in the China Sea. They have been concerned with problems with South Korea and the People's Republic of China.

Japan Deep-sea Trawlers Association represents companies operating large distant-water trawlers, and has been active in negotiations with Mauritania (Chairman of the association served as the Japanese chief delegate). It has made arrangements for exploratory trawl fishing for new grounds, and has engaged in planning the production of pollack minced meat ("surimi").

Except the first two mentioned in the above list, these associations represent the interests of specific fisheries and provide a convenient means of communication between the government and industry in connection with international negotiations involving such fisheries.

IMPACT OF JAPANESE FISHING

The expansion of the Japanese and Soviet fisheries has caused more international fishery problems than any other single factor. To be fair, some credit should be given to these two nations for their contribution towards development of new fishery resources all over the world. Japan and the Soviet Union, for example, have developed new resources in the Bering Sea and

adjacent areas which now support an annual combined yield of perhaps 3 million metric tons and which would have remained unexploited or grossly underexploited without their effort. Japan has developed the tuna resources of the world ocean exploitable by longline. Again along with the Soviet Union, Japan initiated large-scale exploitation of groundfish resources along the west coast of Africa. The Soviet Union has been most active in developing new resources in the northwest Atlantic area. Japan has developed other resources, though not as great as those mentioned above, in various parts of the world.

On the international scene, however, Japan has seldom been given credit for her contribution towards resource development, for the impact of Japanese distant-waters fisheries on the resources in international waters, some of which are also utilized by coastal states, was such that many nations look upon Japanese fishing, along with Soviet fishing, as one of the major factors responsible for the depletion of fishery resources on a global basis. There are many obvious cases in which Japan should be blamed for overexploitation of the resources that were either utilized by other states at the same time or were considered important potential resources for them. Japan and the Soviet Union are largely responsible for the present state of the Antarctic whale stocks; Japan obviously overexploited many of the important stocks in the East China Sea; she overfished the yellowfin sole stock in the eastern Bering Sea, which was also an important resource for the Soviet Union; the impact of offshore salmon fishing on the Soviet salmon stocks is apparent, although no critical assessment has been carried out; many of the crab stocks in the Bering Sea and Kamchatka have been overexploited to varying degrees; some of the stocks of porgies (sparids) in West Africa have been overfished by the trawl fisheries of Japan and some other nations.

In other instances, Japanese fishing has not had any substantial effect on the fisheries of the coastal states concerned, as is the case with the pollack fishery in the Bering Sea, much of the tuna and skipjack fishing, deepwater trawling, fishing for cuttlefish and octopus in northwest Africa, herring fishing in the eastern Bering Sea, squid fishing off New York, etc. But even in those cases, the way new resources have been developed by the Japanese looks frightening to many other nations. A new resource may be exploited to a maximum level within several years, sometimes in 2 or 3 years. Emphasis shifts from one resource to another, or from area to area. The way Japanese trawl fisheries in the Bering Sea and adjacent areas are being expanded mainly based on one species, pollack, makes biologists wonder how long the resource can support the fisheries and what would happen if the pollack stock collapsed suddenly.

This new pattern of fishing, characterized by concentration of effort through large fleet operations and shift of emphasis from one resource to another, may not necessarily be a bad strategy from the point of view of maintaining the total production and the profitability of the industry. But it is not acceptable to many other nations because it is contradictory to the established principles of management based on the concept of maximum sustainable yield and, more important, because such a pattern of fishing can be adopted only by nations having well-organized distant-water fisheries. If a nation is unable to participate in the utilization of a resource for technological or economic reasons, she would rather keep it undeveloped than see some other nation exploit it.

There is little doubt that the development of Japanese and Soviet distant-water fisheries has had very appreciable effects on the international fishery regimes. The impact of these fisheries, whether real or imaginary, has been one of the major factors motivating unilateral jurisdictional claims by coastal states. This applies, for example, to actions taken by the United States, Canada, South Korea, some of the Latin American nations, many of the West African states, and even some of the Southeast Asian nations. Even the Soviet Union has taken unilateral actions to protect its fisheries against Japanese high seas activities. In addition to these events, the expansion of Japanese and Soviet fisheries has been at least partially responsible for a worldwide trend for coastal states to justify various forms of jurisdictional control as effective means to deal with international fishery prob-

lems. Whether or not the Law of the Sea Conference can produce a general agreement on this matter, some principle to the above effect is likely to emerge as a consensus of the majority. Exactly to what extent the development of distant-water fisheries has contributed to this general trend is difficult to assess. It should also be pointed out that some of the European nations, particularly the east European, have followed the example of Soviet fishery development, though on a smaller scale, and have accelerated the trend for extension of coastal jurisdiction.

FUTURE PROBLEMS

CHANGES IN REGIMES FOR FISHERIES

The purpose of this section is to make predictions, based on past performance, on how the Japanese government and industry might respond to possible changes in international regimes for marine living resources.

First, a brief analysis of the changes in international regimes that are most likely to take place appears appropriate (Kasahara, in press). The first preparatory meeting of the Law of the Sea Conference (scheduled for 1973), held in March 1971, made it clear that fishery problems were among the most controversial issues concerning uses of the ocean. One of the reasons for this is the fact that fisheries are important to many of the developing countries, which comprise the overwhelming majority of United Nations membership. Another factor, which may be more important, is the very nature of fishery problems. It is perhaps useful to note how well some of the major uses of the sea have been served by the existing regimes based largely on the traditional concept of free access. These include transportation, which is the most important use of the sea, communication, scientific research, and recreation. Even the exploitation of mineral resources has not caused insolvable international conflicts. Although developing nations might look upon such freedoms as inequitable because of their limited participation, little real damage has been done in those aspects of use of the sea. The major exceptions to this general notion are fishing and pollution. Except for pollution from sea accidents, most of marine pollution originates in areas within the limits of national jurisdiction rather than beyond. This leaves fishing as the most controversial issue.

Free access to fishing on the high seas may have served for increasing food production from the sea, but it has resulted in numerous international conflicts and necessitated almost continuous negotiations between nations all over the world. Most of the actions taken to extend national jurisdiction in one form or another have been motivated by a desire to control use of living resources. Fishery interests have also created such new concepts as an exclusive fishery zone, preferential rights of coastal states, as well as the allocation of resources in international waters.

Judging from the nature of recent fishery conflicts and discussions in the United Nations system, one of the predominant trends will obviously be further extension of coastal jurisdiction over the exploitation of living resources. Such a trend will continue regardless of the outcome of the Law of the Sea Conference. Extension of coastal jurisdiction might take the form of broader territorial zones, or preferential rights of coastal states. National claims might also be expanded through a new definition of living resources subject to the existing continental shelf convention and/or a new sea-bed treaty now under consideration. It is also possible that some nations might translate the new regime for sea-bed resources into a regime for the control of living resources in superjacent waters.

There is no question that most of the developed nations would prefer a relatively narrow territorial sea as a general rule from the point of view of minimizing potential hazards to important nonextractive uses of the sea, particularly shipping and navigation. The probability of coastal states taking unilateral actions to restrict the right of passage for nonmilitary purposes is rather remote, since practically all nations are beneficiaries of this right, and such actions would result in retaliatory measures of various kinds. Nevertheless, under certain circumstances, some nations might possibly take such actions for economic gains. However small

the probability might be, the stake is big enough for a substantial number of nations to try to block a proposal for a territorial sea wider than 12 miles, or, failing this, to refuse to sign any treaty containing such a provision. Thus, chances are slim for an *effective* global treaty specifying a territorial sea broader than 12 miles to come out of the proposed 1973 conference. This will not, of course, prevent some nations from extending their territorial seas through unilateral claims. If any effective global agreement on fishery matters should come out of this conference, however, it would be based on the principle of separating out the question of jurisdiction over fisheries from the total package of national jurisdictions comprising sovereignty.

The conference may not result in an overall agreement on fishery issues, but it is quite likely that there will be a general recognition of special rights of coastal states in terms of exclusive fishery jurisdiction or other forms of preferential allocation of resources. Such a principle will be supported not only by developing nations but also many of the developed nations.

One way of protecting fishery interests of coastal states beyond the territorial sea would be the recognition of exclusive fishery jurisdiction within a certain zone, perhaps defined in terms of a fixed distance and/or a depth. It would be up to the particular coastal state whether it chooses to allow foreign fishermen to fish within the zone under conditions set by the coastal state. Some coastal states might prefer to allow foreign fishing for the resources that are not utilized or grossly underexploited by their own fishermen, probably charging foreign vessels a substantial fee. Arrangements might also be made for such resources to be developed from coastal bases as a condition for allowing foreign fishing.

Another way of protecting the interests of coastal states would be for coastal fisheries to be given preferential rights (including a right to adopt and implement conservation measures which would be binding on foreign vessels) to all resources within a certain zone beyond the territorial limit. This would involve problems of determining what portions of such resources or catches therefrom should be allocated to the coastal fisheries concerned, including the question of whether the coastal state should have a right to control the exploitation of the resources that are not used by them to any substantial degree. Under this principle, the formula to be adopted would perhaps vary from case to case. Preferential fishing rights might also be applied to specific resources important to the coastal states without establishing a fixed zone. This would involve such additional questions as the determination of major areas of distribution of the resources concerned, and the effect of foreign fishing for other resources on the particular resources in the same area.

Among the three alternatives mentioned above, more nations might favor the first to ensure a greater degree of control and simplicity of implementation. The main question in this case would be how the zone should be defined. Some of the nations supporting this idea may still be thinking in terms of a distance of 12 nautical miles from the shore for their exclusive fishery zone, with a narrower territorial sea. Some others are apparently considering varying distances to meet the specific situations. A substantial number of nations seem to favor much greater distance, up to 200 miles, and/or to the outer edge of the continental shelf.

A small number of nations might prefer preferential fishing rights for specific resources that are important to their coastal fisheries. This would be a rather complex concept and a variety of problems would arise from its implementation. Many different formulae could be considered. The existing arrangement for yellowfin tuna in the eastern tropical Pacific may fall in this general category in that allowance is made, within the total catch limit, for vessels of smaller carrying capacities. Various bilateral fishery agreements between the United States and nations operating distant-water fisheries off her coast also include provisions for reducing the adverse effects, on coastal fisheries, of foreign fishing on the high seas. The treatment of anadromous fishes, particularly salmon, and marine mammals returning to land for breeding might also be considered a special case in this general category. Different formulae are in practice to handle such a case. For North American salmon, the absten-

tion principle prohibits fishing by Japan in the eastern half of the North Pacific and Bering Sea. Catches of Asian salmon, on the other hand, have been shared by the Soviet Union and Japan. A system of product distribution has been applied to the harvesting of North Pacific fur seals.

Along with the general trend of extension of coastal jurisdiction, there will also be a continuing trend for more bilateral and multilateral fishery agreements between the nations directly concerned. International agreements solely for conservation, that is, for the purpose of maximizing the total catch, have become less and less attractive to most nations, and emphasis has shifted to arrangements combining systems of allocation with conservation measures. The question of national quotas, particularly for the heavily exploited stocks, will undoubtedly become one of the most critical issues of fishery negotiations in the future. National quota systems are now being discussed even by some of the international commissions which originally did not envisage them, as is the case with the Inter-American Tropical Tuna Commission or the International Commission for the Northwest Atlantic Fisheries. There is no established set of principles as to how the allowable total catch from a stock or stocks should be divided among the nations exploiting such a stock or stocks in waters beyond the limits of national jurisdiction, nor as to what allowance should be made for new entry.

It is not very likely that the Law of the Sea Conference would come up with any specific formula to divide the limited catch. It is possible, however, that discussions at the conference might result in the general acceptance of the establishment of national quotas as a principle of international regulation of fisheries without spelling out details to implement it (such details would be left to bilateral or multilateral agreements between the countries concerned).

In any case, changes likely to take place in the regimes for regulation of fisheries, with a predominant trend for extension of national jurisdiction by coastal states, may result in more international negotiations rather than less. In many parts of the world, such as Southeast Asia, the Gulf of Mexico and the Caribbean, the South Pacific Islands, West Africa, or even in much of Europe, the question of determining the boundaries between areas of national jurisdiction of neighboring states would become enormously complicated and, in some cases, might never be solved. Negotiations for the handling of historical rights of noncoastal states, as well as of neighboring coastal states, in the extended area of national jurisdiction of each state, would also take time. In many regions, regional arrangements of various kinds would have to be negotiated among neighboring coastal states to accommodate each other's fishing activity. Without such arrangements, the development of the fisheries of coastal states would be hampered greatly, and the proper management of stocks of fish crossing several national boundaries would become impossible. In the present political environment, I doubt that the countries concerned could agree to a single regional convention for each region. In most areas, a complex network of bilateral and semiregional agreements would develop. The enforcement of these arrangements would also be difficult and costly.

POSSIBLE RESPONSE

The question of how Japan might respond to likely changes in international regimes for fisheries is, to a substantial degree, answered by what she has done in the past in response to various claims by other nations (see section on International Arrangements). If the Law of the Sea Conference results in a global convention providing for extensive coastal jurisdiction or broad preferential rights of coastal states, it is unlikely that Japan will be a party to such a convention. She would then regard actions taken by member states of the convention as unilateral. In the past, Japan has responded to unilateral actions in a variety of ways. When she did not have much vested interest in the zone claimed and the nation claiming the zone was not prepared for negotiating the issue, Japan voluntarily refrained from fishing in the zone while refusing to recognize the claim. When her vested interest was very substantial, Japan entered into negotiations with the country concerned. In some cases, such as the Japan-South

Korea controversy, the Japanese government did not stop fishing vessels of its nationals from entering the claimed zone, resulting in the seizure of many vessels. In most cases, however, practical arrangements of various kinds were agreed upon, sometimes after long negotiations, as described before. Japan has not challenged any fishery claim by force, and, except for the Japan-South Korea and Japan-Soviet controversies, no real diplomatic crisis has developed from fishery issues.

The future trend in this respect will be about the same. Japan would do her best to protect her fishery interest against unilateral claims with whatever trade offs available to her, both within and outside the purview of fisheries, but would still seek a pragmatic solution to settle the issue. If Japan has no vested interest in the area claimed, she might voluntarily refrain from entering the zone for fishing while officially refusing to recognize the claim. The same would perhaps apply to Japan's reaction to claims based on the concept of preferential rights of coastal states.

Such concepts as the allocation of resources, the division of catches therefrom, or the distribution of benefits, have already been applied extensively to fishery arrangements involving Japan. Although Japan would not recognize these as internationally accepted legal concepts, she would not object to practical arrangements which would have the same effects. The application of a limited entry system has never been a problem to Japan because of the very nature of her domestic regulations, as outlined in the introduction of this paper. In most of the bilateral agreements she has made so far, the number (and in many cases the size as well) of the vessels to operate in a designated area is limited.

Any substantial change in the definition of shelf resources to include more living resources currently exploited would not be recognized by Japan officially. The main reason for Japan not to sign the 1958 continental shelf convention was the inclusion of living resources. The pattern of bilateral negotiations for problems that might arise from this source would be about the same as that for problems from extended fishery jurisdiction. She would do her best to protect the vested interest of her fishing industry.

The possibility of general recognition of a special right to anadromous species, particularly salmon, would be a matter of great concern to Japan, as high seas salmon fishing is still one of the most important sectors of the Japanese fishing industry. During the Law of the Sea Conference, the establishment of a special right to anadromous species may be proposed by some nations as one of the principles of international regulation of fisheries. This might receive rather broad support, not only because of problems of Pacific salmon but also in view of recent developments in offshore salmon fishing in the Atlantic. Again, Japan would not join a convention including such a provision. But if the United States, Canada, and the Soviet Union should claim, on the basis of such a convention, a special right to anadromous species for the main purpose of eventually eliminating high seas salmon fishing, Japan would be in a difficult position to protect her interest in salmon fishing.

The idea of establishing a world agency for regulating all high seas fisheries has been talked about by idealistic people, but by now it is widely recognized that this is not feasible, nor even desirable. We can pretty well eliminate this possibility from our consideration of fishery problems in the foreseeable future.

In short, it is unlikely that Japan could take any definite course of action to cope with an increasing number of international problems she is going to face. She must be prepared for more and harder negotiations to find a practical solution to each of the problems. In the North Pacific, Japan will have to keep negotiating with the Soviet Union for salmon, crabs, and herring, and probably for some of the groundfishes in the future. Negotiations have become increasingly difficult as additional regulatory measures have been proposed by the Soviet Union every year. As the U.S. king crab fishery in the Bering Sea is expanding with the Japanese quota being reduced, the future of the Bering Sea king crab fishery also looks bad. Continuous pressure will come from the United States and Canada to provide their coastal fisheries with a

greater amount of protection against Japanese fishing for groundfishes and shrimp. Pollack, the main species for the trawl fisheries in the Bering Sea and Kamchatka waters, might become a serious international problem in the near future. Japanese fishing pressure is still mounting; the Soviet catch is increasing; South Korea is building a number of stern trawlers in Japan with a view to rapidly increasing her participation in pollack fishing. The Japanese trawl fishery along the west coast of Africa will face further international problems as more African nations take measures to extend fishery jurisdiction. Most of the bilateral agreements Japan has concluded in recent years are of short duration, and it may be difficult to continue these on the same terms.

The Japanese tuna industry might still be able to compete with the Taiwanese and Korean fisheries by taking advantage of rapidly expanding domestic markets, but a substantial increase in the catch of the longline fishery is not likely. Major efforts are being made to develop a purse-seine fishery similar to that of the United States and to increase the production of skipjack, which is at present an underexploited resource; but international regulations will gradually be applied to many of the tuna fisheries. In the eastern tropical Pacific, the present pattern of tuna fishing is likely to lead to a system of national quotas. Tuna fisheries in the Atlantic will also be subject to some international regulatory system in the future. Eventually there might be a regime of worldwide regulation covering all major tuna fisheries. Trawl fishing in the Northwest Atlantic will also be subject to further restrictions through bilateral and multilateral arrangements. Whaling both in the Antarctic and the North Pacific will have to be further curtailed.

International fishery problems faced by the Soviet Union are not too different from those confronting Japan, except in the Northwest Pacific where the Soviet Union finds herself in the position of a coastal nation seeking protection against Japanese fisheries. It is interesting to note that their responses to unilateral claims have not been too different from those of Japan.

FUTURE OF THE INDUSTRY

The phenomenal growth of the Japanese economy has greatly increased demand for high-quality foods, particularly animal protein products. The per capita consumption of animal protein increased by 19% in the 5-fiscal year period of 1963-68. About 58% of the animal protein intake is still from seafoods, including whale meat. During the same period, the per capita expenditure for fishery products increased by 10% per annum in cities and 13.2% per annum in rural areas (Anonymous, 1969). Markets have also developed for a greater variety of fishery products. Imbalance between demand and supply has been increasing constantly, pushing up prices sharply. Pressure for increased fish supply is still quite strong in Japan.

Domestic Production

What alternatives are available for Japan to meet this problem? First, let us examine the possibilities of increasing the domestic supply of fish. Figure 16 indicates the trend for production by four sectors of the Japanese marine fishing industry. Divisions between the sectors, except aquaculture, are somewhat arbitrary.

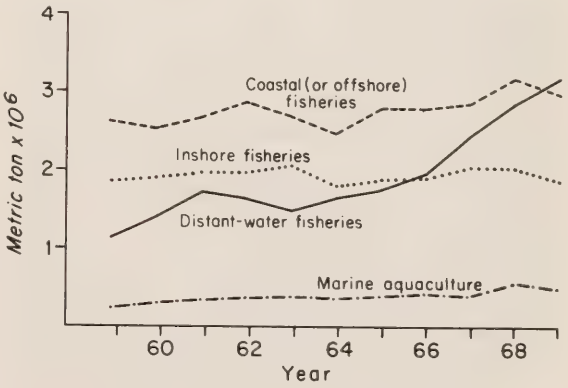

FIGURE 16.—Production of four sectors of the Japanese fishing industry 1959-69 (from Ministry of Agriculture and Forestry, 1971). Division between inshore fisheries and coastal (or offshore) fisheries is somewhat arbitrary. Distant-water fisheries include trawl fisheries in the China Sea.

The total production of inshore fisheries has stayed about the same for the last 10 years, a little less than 2 million metric tons. The total catch of coastal fisheries (called "offshore fisheries" in Japan) has shown a substantial increase, but has been influenced by fluctuations of a few pelagic species. (Mackerels and common squid, for example, account for a sharp increase in 1968.) Distant-water fisheries have contributed greatly to a general increase in production during the last 10 years, but pollack account for the largest portion of the growth. In fact, many of the other distant-water fisheries have shown a decline in the most recent years. Pollack are largely processed into minced meat and fish meal. The domestic production of fish meal has also increased rapidly during the same period.[31] Fish meal is manufactured on factoryships, now mainly from pollack, as well as on land, from mackerel, some other coastal pelagic species, and pollack.

Inshore fisheries.—This sector consists of fishing by small vessels (particularly draggers), coastal traps, beach seines, and other miscellaneous methods including collection of bivalves and seaweeds. Virtually all stocks in inshore waters are exploited very intensively, and no increase in production would be possible by further intensifying fishing efforts. Theoretically it might be possible to improve the fisheries in this category by introducing better management measures, but it would create enormous social and economic problems. The fisheries are tightly controlled by the long-established fishing right system largely operating through cooperatives.

This sector of the industry has always presented difficult social problems due to low productivity (efficient fishing methods are usually outlawed) and overemployment. Unlike farmers around urban areas, who have become rich by selling their land for industrial or residential use, these fishermen have nothing to cash in. Social problems of small fishing communities along the Japanese coast will only be solved gradually by young people being absorbed in manufacturing industries. The industrialization and urbanization of the coastal zone is becoming a real threat to inshore fisheries, particularly those in bays and estuaries. Inshore fisheries are still important in Japan for providing consumers with fresh, high-priced seafoods, but the possibility of increasing their total production has to be written off.

Coastal (or offshore) fisheries.—This category includes all fisheries carried out by medium-sized vessels. They include Danish seining, pair trawling, purse seining, saury fishing, tuna longlining by smaller vessels, salmon fishing by smaller vessels, skipjack fishing by smaller vessels, pole-and-line fishing for mackerel, squid fishing, and others. Some of these fisheries are conducted in fairly distant waters, for example, tuna and skipjack fishing or offshore saury fishing. Except in the last 2 years, this sector has produced the greatest proportion of the total catch of the entire Japanese fishing industry.

While the catches of groundfishes around the Japanese islands have been relatively stable, under very strong fishing pressure, the catches of coastal pelagic species have fluctuated greatly as outlined in Other Fisheries, pages 243 to 245. All of these species have been exploited very intensively. Although Japanese scientists do not agree on the causes of the declining catches of some of these species, particularly sardines (*Sardinops*) and saury, overfishing is a strong possibility. The causes of a rapid increase in jack mackerel during the late 1950's and early 1960's and in mackerels (mainly *Scomber japonicus*) in the late 1960's are also unknown. This sector of the industry will continue to face large fluctuations in the catches of major pelagic species, but a long-term increase of the total catch is unlikely. The total production of major coastal pelagic species, including mackerels, jack mackerel, anchovy, saury, sardines (now very insignificant), and squids during 1956-69 is shown in Figure 17. (The figure includes catches by inshore fisheries.) The introduction of better methods of resource manage-

[31] As in most other industrialized countries, demand for fish meal as animal feeds has risen sharply and has been met mainly by domestic supply and partly by imports. Domestic producers have been protected by an import quota.

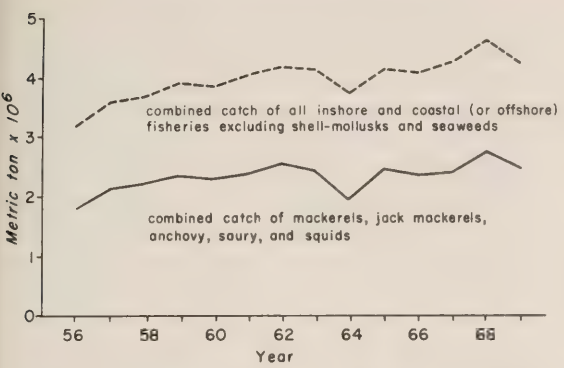

FIGURE 17.—Combined catch of mackerels, jack mackerels (including *Decapterus*), anchovy, saury, and squids, 1956-69 (from Ministry of Agriculture and Forestry, 1971).

ment does not appear practical at the moment, because of the complexity of regulations under the licensing system and the lack of understanding of the causes of sharp decreases or rapid increases in the abundance and catch of coastal pelagic species.

In the long run, however, this is one area in which substantial improvements in efficiency, and possibly in total production, might be possible largely by reducing fishing effort. This applies to both demersal species and coastal pelagic species. This would require major political decisions, with great social and economic implications. Such a process would take many years in any case.

Distant-water fisheries.—Although the total production of distant-water fisheries has increased very sharply, the catches of many fisheries in this category have actually been on the decline in recent years, due to international regulation, decreases in abundance of many stocks, and increasing competition with other countries. The total catch of the mothership salmon fishery in the Northwest Pacific has decreased from 71,000 metric tons to 40,000 tons in the last 10 years. (That of the land-based salmon gill-net fishery has decreased from 85,000 tons to 55,000 tons in the same period.) The king crab catch by the mothership crab fishery has declined from 15,000 tons in 1964 to a little over 9,000 tons in 1969. The loss has been compensated by a sudden increase in the tanner crab catch in the last 3 years. The combined catch of all home-based tuna longliners has declined from the peak of 386,000 tons (including nontuna species, such as billfishes, swordfish, and sharks) in 1962 to 317,000 tons in 1969, and that of foreign-based operations (in the South Pacific, Indian Ocean, and Atlantic) from 118,000 tons in 1965 to only 28,000 tons in 1970. The catch of the mothership tuna fishery (with deck-loaded catchers) has also decreased, from 68,000 tons in 1964 to 38,000 tons in 1969. The long-established pair-trawl fishery in the China Seas has been at about the same level for the last 10 years, with a slight decline in the most recent years. The total catch of the trawl fisheries in the Atlantic increased rapidly until 1967 and has stayed at about the same level since then.

The sharp increase in the total catch of distant-water fisheries, shown in Figure 16, is accounted for mainly by the expansion of the trawl fisheries in the northern North Pacific. The catch of the mothership trawl fishery has increased from 169,000 metric tons in 1959 to 862,000 tons in 1969. The catch of independent trawlers increased from 2,000 tons to 373,000 tons in the same period, and that of "Hokutensen" from nothing to 768,000 tons. The mothership trawl fishery in the Bering Sea first depended mainly on yellowfin sole, but emphasis shifted to other species, particularly pollack, when the flounder stock in the eastern Bering Sea declined sharply.

Since the introduction of minced meat ("surimi"), the proportions of pollack in the catches of these trawl fisheries have jumped up. As of 1969, 678,000 tons out of 862,000 tons caught by the mothership trawl fishery were pollack. Corresponding figures for independent trawlers were 200,000 tons out of 373,000 tons (they take substantial quantities of ocean perch in the Aleutian and the Gulf of Alaska). Those for Hokutensen were 670,000 tons out of 768,000 tons. The total catch of pollack by distant-water fisheries has risen from 33,000 tons in 1959 to 1.55 million tons in 1969. The corresponding figures for the coastal fisheries are 343,000 tons and

396,000 tons. The pollack catch is still increasing; several 5,000-ton class vessels, newly built, are coming into operation. The recovery rate of minced meat from pollack is relatively small, probably between 20 and 25%, and the remainder goes to fish meal and oil. But the price of pollack surimi, used for making fish cakes ("kamaboko," "chikuwa") and other products, is so high that it makes all the difference in the profitability of the trawl fisheries in the northern areas. The price of fish meal is also high, around $200 per ton. Although imports of fish meal are scheduled to be liberalized this year, a high import duty will be levied when imports exceed a certain quantity still to be fixed.

Search for new distant-water fishing grounds continues, and there have been some developments in this area, such as deepwater trawling around the mid-Pacific islands, squid fishing off the Atlantic coast of the United States, trawling in the Gulf of Aden for sea breams and cuttlefish, or fishing for barracouta (*Leionura*) off New Zealand. Although further effort will be made in this direction, most of the abundant resources of traditional species are likely to be in areas relatively close to the coasts of foreign countries. Thus, uncertainties about the future regimes for fisheries are a discouraging factor. Trawling in waters deeper than 500 m, expansion of skipjack fishing, particularly in the tropical Pacific, and the development of cephalopod resources in various parts of the world, are good possibilities. In general, however, prospects for further expansion of Japanese distant-waters fisheries to harvest conventional species by known methods do not appear bright.

Aquaculture.—As shown in Figure 16, the yield of marine aquaculture has been increasing steadily. Since aquaculture includes a variety of things, we must examine a breakdown of the total yield, which is shown in Table 7. Out of the total of 473,000 metric tons produced by marine aquaculture in 1969, 245,000 tons were oysters *with shell.* The equivalent figure for oyster meat is estimated at 37,000 tons. Next comes laver ("nori," *Porphyra*) at 134,000 tons; "wakame" (also seaweed, *Undaria*) accounts for 60,000 tons; the remainder, 34,000 tons, consists

TABLE 7.—Aquaculture production, excluding pearl culture, in 1969.

Aquaculture	Live weight
	metric tons
Marine:	
Laver	134,320
Wakame	59,821
Oysters (meat weight)	(36,988)
Oysters (shell weight equivalent)	245,458
Yellowtail	32,613
Puffer	52
Other fishes	481
Octopus	50
Shrimp *(Penaeus japonicus)*	295
Spiny lobster	2
Swimming crab	1
Other aquatic animals	102
Total	473,195
Freshwater:	
Trouts	10,254
Carps	13,971
Crucian carp	1,776
Eels	23,276
Other fishes	2,762
Total	52,039

Source: Ministry of Agriculture and Forestry (Japan) (1971).

of cultured fishes and various invertebrates. Thus, in terms of animal protein products, 37,000 tons of oyster meat and 34,000 tons of fish and other animals are all that is produced by marine aquaculture. Aquaculture for oysters and laver can still be expanded. It is facing, however, mounting problems arising from the industrialization of the coastal zone, particularly pollution and land reclamation. The main fish species for marine aquaculture in Japan is yellowtail (*Seriola*), others being quite insignificant in quantity. Shrimp culture in Japan is advertised all over the world, but actual production in 1969 was only 300 tons.

Freshwater aquaculture produces a substantial amount of fish: 23,000 tons of eels, 14,000 tons of carp, and 10,000 tons of trouts in 1969. The yields of these species have increased very substantially in the last 10 years, but the total production of freshwater fish culture is still a little over 50,000 tons. All aquaculture for fishes and crustaceans, in both seawater and fresh water, is carried out by intensive feeding. In most cases, fishes (largely coastal pelagic species) and fish meal are the main animal protein components of feeds. On a round-weight basis, the amount of feed fish required for yellowtail and eel culture is perhaps 7 to 8 times the amount

of fish produced. It is estimated that the consumption of fish meal for culturing eels and trouts alone might reach 100,000 tons in 1971 (the equivalent of half a million tons in live weight). Fish culture in Japan is obviously a means to produce high-priced products and not to increase the total supply of animal protein from the sea. While demand for cultured fishes remains very strong, the aquaculture of the two most important forms, eels and yellowtail, has a serious weakness. Their young have to be collected from natural waters. The domestic supply of young eels is declining, due at least partly to pollution in estuarine waters, and a substantial quantity is now being imported. The price of elvers is reported to be nearly $38 a pound.

The above review of prospects for expansion of each of the main sectors of the fishing industry indicates that it will become increasingly difficult for the domestic supply of fish to meet the evergrowing demand. In the long run, better management of coastal fisheries may result in a substantial increase in the total harvest, but this is a painstaking and time-consuming process. Further exploitation of resources in distant waters may result in some increase, but the scarcity of readily exploitable resources and uncertainties about international problems are major obstacles. Expansion of aquaculture is possible, but it would have the effect of further reducing the total amount of food fish available as long as fish and fish meal are used as major components of feeds.

Exploitation of unconventional species.—Man will have to make serious attempts to exploit unconventional species in order to sustain a reasonably high rate of growth in fishery production. What is meant by unconventional species is those forms which occur in great abundance in wide areas of the ocean and which are difficult to harvest and market economically with known methods. The utilization of these resources is in a way a continuation of the recent trend for exploiting a greater variety of species. It appears, however, that some technological breakthroughs would be required to begin large-scale commercial exploitation of such forms as the Antarctic krill (*Euphausia superba*) and other larger zooplankton, red crab (*Pleuroncodes*), lanternfishes (myctophids), gonostomatids, deepsea smelts (bathylagids), etc. Large concentrations of lanternfishes have been found in most parts of the ocean. An enormous biomass of bristlemouth (*Cyclothone*) occurs in the tropical Pacific. The abundance of deepsea smelts in the California Current system is well known. Particularly interesting in this respect is the existence of extensive offshore areas of upwelling associated with the equatorial current systems (Cushing, 1969).

The Soviet Union has been making effort to utilize *Euphausia superba* through experimental fishing and processing, with limited success. Japan has a modest program to explore the possibility of using larger zooplankton and progress has been reported in making some products out of euphausiids. Both nations still have a long way to go in this area. Furthermore, fish meal and other products into which these forms might be processed are unlikely to substitute for highly demanded conventional species although they might increase the supply of feeds.

International Business Arrangements

One might think that Japan must have been very active in developing joint ventures and other forms of international arrangements to carry out fishing from the coastal states near the fishing grounds. For a variety of reasons, her activities in this general category have been limited to a few things, such as use of facilities for transshipment of tuna caught by longliners, joint ventures for shrimping, and more recently joint ventures for skipjack live-bait fishing. Japanese trawlers operating in West Africa have been selling some of the catches locally and a few vessels still operate under contracts with local companies.

There are a variety of reasons for the lack of major developments in this general area. In many cases, the local governments establish various requirements as conditions for land-based foreign operations, such as investment in shore facilities or nationalization of equipment and crews. They may be reluctant to make such concessions as tax-free imports of equipment

and supplies. Political instability may make investments extremely risky. As long as the same types of fishing can be carried out by their own boats without heavy local investments, the Japanese companies would prefer not to make complicated arrangements with local firms or governments, except for use of local facilities for transshipment.

A major exception in this regard is shrimping, for most of the rich shrimp grounds are even now within the limits of national jurisdiction of coastal states. The existence of excellent international markets for shrimp makes joint ventures attractive even under difficult local conditions. A number of Japanese companies have recently begun shrimping in the rich grounds of Indonesia, including West Irian. Live-bait fishing for skipjack in areas far from the home islands is another type of operation which has to be carried out from local bases. Joint ventures with Australia (from New Guinea) and Indonesia (from West Irian) are now developing. Transshipping of frozen tuna through foreign bases is an essential part of the worldwide longline fisheries. Trawl fishing vessels in the Atlantic use Las Palmas and Cape Town as their main bases of operation.

The situation is changing, as more and more nations are inclined to extend their national jurisdiction. Already, use of local facilities is a condition for tuna fishing in the Banda Sea under the Japan-Indonesia agreement, and the delivery of catches by some vessels to local facilities is a condition for fishing under the Japan-Mauritania agreement. Payments are involved in both cases.

As far as the industry is concerned, fishing with payments, without further local involvement, might be preferable to other arrangements in many cases. The industry could include the amounts paid (if they are reasonable) in the costs of products and charge them to consumers. The main problem here is the official position of the Japanese government concerning the territorial sea and fishing jurisdiction. Payments could still be made under other names than licensing fees; for example, as payments for use of local facilities. The government of the coastal states, on the other hand, might not agree to such an arrangement which could weaken their positions on jurisdiction. Since there are already precedents of this sort (Indonesia, Mauritania, and Australia), however, this approach may be used more widely in the future.

Another direction in which the industry might move is more direct investments in the prosperous foreign fishing and processing industries. The United States has gone far ahead of Japan in this area. Japan now has a small interest in the Peruvian fish meal industry. I do not quite understand why some of the large Japanese trade companies, which handle various fishery products, have not vigorously explored possibilities of direct investment in foreign fishing industries. The government used to discourage involvement of Japanese firms in foreign fishing ventures for fear of increasing competition with Japanese fisheries. But the main reason may now be that there are not many fisheries in foreign countries which offer long-term returns comparable to those expected from other industries, perhaps with the exception of fish meal and shrimp operations in some areas.

Imports

As shown in Figure 18, there has been a marked increase in imports of fishery products in the last 10 years, while exports have generally leveled off. For many years, however, the Japanese government has imposed rather strict restrictions on imports of fishery products, mainly based on two considerations: the balance of payment and the competition with domestic products. With the foreign exchange surplus increasing at an almost embarrassing rate, the balance of payment is no longer a problem. On the contrary, pressure is mounting for the government to facilitate importation of many items including food in general. Internationally, Japan has been urged by both developed nations (including the United States) and developing nations to relax trade restrictions. Also, the government must explore all means to accelerate foreign currency spending to reduce the rate of increase in the surplus and slow down inflation. Increased imports of food items are generally considered desirable from this point of view.

FIGURE 18.—Imports and exports of fishery products, 1959-69 (from Suisan-sha, 1970). Pearls are excluded. Figures for 1969 are estimates. ¥360 per dollar.

The liberalization of the import of fishery products began only in 1960, and a major change took place in 1961 when a number of fresh and frozen fishes and shellfishes were removed from the list of restricted items. Many items, however, still remain on the list mainly to protect the interests of inshore and coastal fisheries. The Japanese system of control of fishery imports is quite complicated. An attempt is made below to describe it briefly (from Suisan-sha, 1970).

As of 1970, all imports of fishery products fell under two categories: those which are not subject to quotas (Automatic Approval System, abbreviated AA) and those which are subject to quotas (Import Quota System, IQ). Among important AA items are a number of fresh or frozen fishes and shellfishes, including shrimp, tunas (including skipjack), swordfish, salmon, porgies, etc.; most of the canned fishes; and whale meat. Among important IQ items are a variety of fresh and frozen fishes, including herring, cod and pollack, yellowtail, mackerels, sardines and anchovy, jack mackerels, saury, cod (or pollack) roe, herring roe, as well as salted, dried, or smoked products of these species; laver and kelps; fish meal and whale meal, as well as mixed feeds or fish solubles; and fresh, frozen, or dried squid and cuttlefish. As Japan is now a party to IMF (International Monetary Fund) Article 8, all quotas are in principle on a global basis. A special quota system, however, is applied to imports of fishes and shellfishes caught in coastal waters of South Korea; they can be imported within a fixed total value.

In terms of total value, shrimp (from the People's Republic of China, United States, Mexico, Thailand, and a number of other sources) has been the number one import item in recent years. Other important products imported are fish meal from Peru and South Africa, dry laver from South Korea, cuttlefish and octopus from West African fisheries (presumably shipped through Las Palmas), and tunas from Taiwan, Ryukyu, and South Korea.

Reviewing the actual quotas applied, it is obvious that import restrictions are still quite severe for some products. The amount of laver imported from South Korea has been controlled strictly to protect domestic laver culture, which is one of the most important sectors of the Japanese fishing industry. The amount of imported fish meal is also controlled to protect fish meal manufacturing in Japan both aboard factoryships and ashore. In addition, the quantity of fish that can be purchased from foreign countries as raw material for fish meal (mainly pollack from the Soviet Union) is restricted. Some of the products which fetch extremely high prices are also tightly controlled. These include herring roe, as well as herring used for making dry herring and roe, cod and pollack roe, cuttlefish from West Africa, and some others.

Excepting laver, imports from South Korea are decreasing due largely to limited production in Korean coastal waters and growing domestic demand in Korea. In 1970, mackerels and jack mackerels, which had previously been excluded from items to be imported, were added to the list of products under the special value quota. The actual imports of these two forms in 1970 were very little because of strong demand in Korea. Future trend may be for the import of cultured oysters (just started) and clams, since Korea has a great potential for aquaculture in shallow waters. As Korea plans to expand her distant-water trawl fisheries in the North Pacific and West Africa, there may be pressure for increased imports of products from this source. Presumably, they will come under the global quotas of respective items.

Quotas for individual items are determined through consultations between the Ministry of Trade and the Fishery Agency of the Ministry of Agriculture and Forestry. The former normally presses for liberalization while the latter tends to resist it. In the case of fish meal imports, there is a conflict within the Ministry of Agriculture and Forestry, namely between the Fishery Agency and the Livestock Bureau, since the poultry and livestock industries in Japan want complete decontrol of fish meal imports.

Import duties on fishery products are in principle 10% on fresh and frozen items, 15% on salted and smoked items, and 20% on canned and related items. Duties on many AA items have been reduced gradually under the Kennedy Round system.

Further import decontrol is highly desirable and almost inevitable. Fish meal imports are due to be decontrolled, to a large extent, in the near future. The present plan is to determine, through consultations between the Fishery Agency and the Livestock Bureau, the amount of meal to be imported duty free, and to tax heavily any additional imports (in the neighborhood of $56 a ton). The effects of this measure will depend largely on the amount to be fixed for duty-free imports. If the quantity determined is high enough, the net effect will be almost complete decontrol. If, on the other hand, the amount is adjusted to protect domestic manufacturers, the situation will not be too different from what it is now.

A further step which should be considered is the relaxation of restrictions on pollack imports. The Soviet Union now produces a large quantity of pollack (mainly in waters off Kamchatka), 598,000 metric tons in 1969 as compared with 1,944,000 tons caught by Japan. (Including the North Korean catch, the total yield of Pacific pollack probably exceeded 3 million tons in 1970.) Presumably, most of the Russian pollack catch goes into fish meal. If the Soviet Union can export pollack to Japan for surimi manufacturing, the value of the Soviet catch would increase very substantially. The Japanese government allows the import of raw material for fish meal, practically all pollack, within a global quota of 45,000 metric tons. Although it is a global quota, the only country that can export pollack to Japan is the Soviet Union. A further strict condition is attached to pollack imports: fish must be processed into fish meal, fish oil, and solubles aboard Japanese ships before entering Japan. Initially, even production of pollack roe was prohibited, but this restriction was removed later. For the last 7 years, pollack have been purchased in west Kamchatka, the main Soviet fishing area, and processed on a Japanese factoryship. The price has been increasing gradually, and the Japanese company conducting this operation has been requesting the government to allow production of surimi, but this has not been approved. It is very difficult to understand why the processing of only 45,000 tons of pollack into surimi would do any harm to Japanese fishing companies or processors.

The basic question here is far beyond that of manufacturing a small amount of surimi under the present quota. Pollack fishing for surimi production is now the mainstay of the Japanese distant-water trawl fisheries. Demand for surimi is strong, and the pollack catch is going to level off sooner or later. Further intensification of Hokutensen fishing and Soviet fishing, and the expected expansion of the Korean fleet, will result in a sharp increase in fishing intensity in Kamchatka and North Kurile waters. Catch limits will become necessary, and I would not be surprised if the Soviet Union pressed for them in the near future. In the long run, it would be beneficial to Japan to increase, if necessary gradually, the purchase of pollack from the Soviet Union for surimi production. It would help meet growing demand; the value added in processing and marketing would be far greater than the value of raw material realized by the Soviet Union;[32] increased imports from the Soviet Union would perhaps alleviate international fishery problems between the two nations. It is not certain what South Korea will do with increasing pollack catches. As pollack, processed into dry fish, has always been highly valued in Korea (both North and South), it is likely that the

[32] The Soviet Union may already be producing surimi using imported Japanese equipment.

catches will be absorbed in Korean domestic markets. However, the Korean operators might try to export some of their catches to Japan or even develop their own surimi industry.

Further liberalization is in order for the import of products from South Korean coastal fisheries. Pressure from the Japanese laver culture industry is so strong that the Japanese government will not immediately relax restrictions on laver, but the present quota system for non-aquaculture products will become rather meaningless.

Another important item to be reconsidered is herring and herring roe. After the collapse of Japanese herring fisheries (Kasahara, 1961), domestic production of herring (mainly in Hokkaido) has become insignificant. Most of the Japanese catch now comes from waters off the coast of the Soviet Union and from the eastern Bering Sea. To meet part of the demand for herring roe and a dried herring product called "migaki," herring has been imported mainly from the Soviet Union either through transshipment on Soviet fishing grounds or as frozen herring. A small amount of frozen herring has also been imported from Alaska. A separate quota has applied to herring roe, the price of which is extremely high in Japan. Japanese companies initially had difficulties in teaching people in Alaska and Canada how to process herring roe, but the business is now firmly established along the coast from Alaska to the State of Washington. Importation of herring has been done through the Federation of Hokkaido Fishery Cooperatives acting as sole import agent. This system was adopted originally to minimize objections from Hokkaido fishermen. Importation of roe, on the other hand, is done by companies.

Herring fishing off the Soviet coast is now subject to severe restrictions under an agreement concluded in 1971. The amount taken by the mothership fishery in the eastern Bering Sea is still limited. The Hokkaido herring stock shows no sign of recovery. Import quotas are still low, 8,000 tons for herring and 500 tons for herring roe. The Japanese population is suffering from a ridiculously high price of roe. The present total consumption of herring products is only a small fraction of what it used to be before the collapse of the Japanese herring fisheries. Except for protecting the vested interest of Hokkaido fishermen, there is no social or economic justification for continuing the present system. Also questionable is an import quota for West African cuttlefish.

In addition to herring, most of the coastal pelagic species are also on the IQ list, including fresh, frozen, and most forms of processed products other than canned fish. Considering the rather small catches of these species made in the neighboring countries, I doubt that these restrictions have real significance. In short, it is about time for Japan to reconsider all trade restrictions on fishery products with a view to facilitating their import, even at the expense of the temporary suffering of some of the domestic fisheries, for increased imports would be beneficial to the population in general. There is a real danger of many of the fishery products becoming luxury items rather than main sources of animal protein supply for the population. This is already happening to a variety of products which were low- or medium-priced items only 10 to 15 years ago. The rapid development of a modern chicken industry in Japan, combined with the liberalization of meat and poultry imports, may make fishery products less and less important as main sources of animal protein.

Although the import quota system has been a major obstacle to the expansion of fishery imports, there are other problems also. The lack of know-how to produce products suitable for Japanese markets, for example, has made it difficult for many foreign countries to exploit export potentials. Except for such international commodities as fish meal, frozen shrimp, tuna, or canned fish, fishery products sold in Japan are very specific as to the method of processing and the quality of final products. The nature of the difficulty is demonstrated by problems which Japanese companies have encountered in the process of developing salmon and herring roe business in North America. In Peru, where anchovies are extremely abundant and cheap, nobody even thought of developing export business to exploit the Japanese market for boil-dried anchovies ("niboshi"). In the Far East and

Southeast Asia, domestic demand for fish is generally quite strong and most of the catches are consumed locally, except for such high-priced international commodities as shrimp or tuna. Some of these nations, particularly the Philippines and Ceylon, import large quantities of fishery products, some of them from Japan. There is no great surplus of low-priced fish in this general region.

The proportion of the combined value of fishery products in the total export value of Japan has been decreasing steadily, only 2.7% in 1968 and perhaps around 2% by 1971. Major export items in recent years have been frozen tuna, other frozen products, canned tuna, canned salmon, canned mackerel, and other canned products. Domestic demand for tuna is growing. Even canned albacore, which used to be a product entirely for export, is now consumed in a substantial quantity.

The Japanese people are extremely flexible in their consumption of fishes, and there is some demand for just about everything coming out of the sea. There are, however, certain trends of consumer preference that have become fairly obvious in the most recent years. First, demand for high-priced fishery products, such as raw tuna meat (particularly bluefin), shrimps, crabs, certain species of cephalopods, salmon, salmon and herring roe, certain species of flounders, yellowtail, eels, and a variety of species produced in inshore waters, is becoming stronger as the standard of living rises rapidly. Since most of these forms have limited supplies, their prices are pushed up sharply, more or less in proportion to the increase in the per capita income. Second, the sale of frozen seafood is going up very fast. This is, to a large extent, because of tremendous improvements made in recent years in the quality of frozen seafood through the introduction of better equipment. Third, demand for fish ham and sausage, which used to be very high, is now going down. This may be due to a greater consumption of true ham and sausage. Fourth, the production and consumption of traditional fish cakes, such as "kamaboko," "chikuwa," and their relatives using "surimi" as material, have gone up sharply as the supply of pollack surimi increased. Use of other species than pollack for these products has decreased at the same time. Fifth, demand for fish meal as feeds for livestock, poultry, and aquaculture is very strong. It is met largely from three sources: pollack, mackerel, and imports. It is obvious that further increases in fish meal consumption will have to be met largely from imports, although domestic production may also grow further.

Even in Japan, large fluctuations in the catches of pelagic species are real problems. For example, the total catch of saury in 1970 was only 85,000 metric tons, as compared with over half a million tons in 1959, but in value the catch was the second largest in history because of the high price of saury, which used to be one of the cheapest fishes. Much of the sharply increasing catch of mackerel has gone into fish meal and oil, with smaller quantities used for direct consumption and canning, the latter mostly for export.

Conclusions

Examining sector by sector, the future of the Japanese fishing industry in general, and distant-water fisheries in particular, does not seem bright. Possibilities for further expansion are limited.

In inshore waters, major efforts are required to minimize the effects of pollution on the productivity of fishing and aquaculture. For coastal and offshore fisheries around the Japanese islands, better management could improve the efficiency of fishing and perhaps total production. The desirability of further decreasing the fishing effort of coastal trawl fisheries is obvious. For coastal pelagic species which make up the greatest portion of the catch from waters around Japan, management strategies based on scientific research have not yet been established, and the fisheries are always subject to large fluctuations in the catches of a few important species.

Distant-water fisheries are facing more and more difficult international problems, and due to a general trend of extension of national jurisdiction, further restrictions are expected. More exploratory fishing (particularly deepwater trawling), joint ventures, fishing in waters of national jurisdiction under conditions set by

coastal states, and development of foreign fisheries through investment by Japan, provide partial answers, and these lines will undoubtedly be pursued. The period of rapid expansion of distant-water fisheries, however, is practically over. The pollack stocks in the North Pacific, on which almost the entire Japanese trawl fisheries in that region depend, are being fished with increasing intensity. With the expansion of Soviet fishing and the entry of a large Korean trawl fleet, problems of conservation and allocation are likely to become major international issues in the near future.

Japan has made little progress in the exploitation of abundant resources of unconventional species. Although such a possibility might be explored more vigorously in the future, it would not solve most of the problems faced by the fishing industry. Further decontrol of the import of fishery products and increased import quotas will provide effective means to meet immediate problems of supply shortage and high prices. In general, too, the future of the Japanese fishing industry should be considered in the context of the rapidly expanding economy of this highly industrialized country. Labor shortage will become further acute, making many types of fishing economically infeasible. Japan, however, has two advantages over many of the other nations: the government has effective means to control the industry and the nation has strong domestic demands for a great variety of fishery products. The Japanese fishing industry will continue to be a competitive one on the international scene for some time to come although it will have to undergo many changes to meet new problems.

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MIGRATION AND DISTRIBUTION OF WHITE MARLIN AND BLUE MARLIN IN THE ATLANTIC OCEAN[1]

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ABSTRACT

Migration and distribution of white marlin, *Tetrapturus albidus* Poey, and blue marlin, *Makaira nigricans* Lacépède, in the Atlantic Ocean are discussed on the basis of tagging data (western North Atlantic, 1954-May 1970) and statistics of the Japanese Atlantic longline fishery (1956-67). White and blue marlins are widely distributed over the warmer waters of the Atlantic. Seasonal concentrations occur in certain areas, especially in the western Atlantic.

In the North Atlantic one group of white marlin summers off the U.S. middle Atlantic coast. In the fall fish of this group migrate offshore, then south to winter off the north coast of South America. In the spring these fish return north along or through the Antilles and the Bahamas. Tagged fish from this group were recaptured after up to 4 years at liberty; the returns suggest that the annual mortality is between 14% and 39%. There are apparently other groups of white marlin in the North Atlantic that move seasonally between various localities, but these movements have not been fully defined. An apparently separate population of white marlin concentrates in the eastern South Atlantic Ocean in winter and in the western part in summer.

Blue marlin concentrate in the Caribbean Sea, the Gulf of Mexico and the North Atlantic south of lat 30°N, from June through October, and in the western and central South Atlantic between lat 10° and lat 20°S from February through April. These concentrations probably represent distinct spawning populations.

The white marlin, *Tetrapturus albidus* Poey, and the blue marlin, *Makaira nigricans* Lacépède (family Istiophoridae), are distributed widely in the Atlantic Ocean. Their distribution and habits are of interest because they are important game fishes and because they are taken by commercial longline fisheries.

Few studies have been made of the migration and distribution of either species in the Atlantic Ocean. Gibbs (1957) described in detail the distribution of white marlin in the Gulf of Mexico from catch records of the U.S. exploratory fishing vessel *Oregon*. Squire (1962) described the distribution of white and blue marlins in the western North Atlantic, based on longline catches of exploratory fishing vessels. De Sylva and Davis (1963) reported on their studies of the white marlin sport fishery off the middle Atlantic coast of the United States. Nakamura, Iwai, and Matsubara (1968) gave a general review of the billfishes of the world.

Ueyanagi et al. (1970) described the distribution, spawning, and relative abundance of billfishes in the Atlantic Ocean; this comprehensive work is based mainly on the results of the Japanese longline fishery and of cruises by Japanese research vessels.

Other reports are based mainly on incidental collections or the results of scattered fishing activity (LaMonte, 1955, 1958a, b; Erdman, 1956, 1962; Krumholz, 1958; Krumholz and de Sylva, 1958; de Sylva, 1958, 1963; Rodriguez-Roda and Howard, 1962; and Talbot and Penrith, 1962).

Sportsmen participating in the Cooperative Game Fish Tagging Program of the Woods Hole

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Oceanographic Institution began tagging marlins and other pelagic fishes in the western North Atlantic in 1954. Preliminary results of the program, pertaining to marlins, were described by Mather (1960, 1967, 1969). In 1956, Japanese longline vessels began fishing for tunas and billfishes in the Atlantic Ocean; this fishery soon expanded to cover all of the tropical and temperate Atlantic. Tag returns and records of catches from the longline fishery have provided detailed data on the distribution, movements, and relative abundance of white and blue marlins in the Atlantic. The results of our study of these data are presented here.

SPORT FISHERY

Sport fishing for marlins and other big game fishes developed along the Atlantic coast of North America and off the Bahamas and Cuba during the 1930's (Figure 1). After 1945, fishing spread to the Gulf of Mexico, the Caribbean, and more distant areas. The growth of the fishery was aided by the widespread prosperity of the era and by improvements in fishing boats and equipment. More white marlin than blue marlin are taken by sportsmen; however, the comparative scarcity and the challenging size and power of blue marlin make them the more highly prized trophy.

White and blue marlins share a vast habitat in the Atlantic Ocean. The white marlin ranges farther into the temperate zones during the warm seasons and congregates seasonally in certain coastal areas in much greater numbers than does the blue marlin. Along the east coast of the United States, white marlin are abundant during the warm season from Cape Hatteras, N.C., north to Cape Cod, Mass., but blue marlin are rarely caught north of Cape Hatteras.

Fishing for white marlin off the middle Atlantic coast of the United States originated in Maryland in 1935, and spread to Cape Hatteras and Cape Cod. The greatest fishing effort and the largest catches are still made off Maryland, Delaware, and adjacent parts of New Jersey and Virginia. The major fishing centers are Ocean City, Md., and the New Jersey ports from Cape May northward to Atlantic City. The most productive fishing grounds are Baltimore and Wilmington Canyons. Boats from nearly all ports on or near the Atlantic Ocean from northern Virginia to Cape Hatteras take white marlin, but Oregon Inlet, N.C., is the major fishing center south of Ocean City. White marlin are relatively scarce in coastal waters off northern New Jersey and western Long Island, N.Y., but often provide good fishing at Hudson Canyon, and from eastern Long Island to Nantucket, Mass., the northeastern limit of their coastal range. As noted above, the occurrence of white marlin from Cape Hatteras to Cape Cod is generally limited to summer.

The first sport fishery for blue marlin off the U.S. coast developed at Hatteras, N.C., in the late 1930's. Another major center for blue marlin fishing off North Carolina is at Morehead City, also mainly in late spring and summer.

White and blue marlins are occasionally taken off southeastern Florida and the Florida Keys, usually by anglers seeking sailfish, but the number caught is small compared to the fishing effort. The best fishing for white marlin in the Florida area is in spring.

Marlin fishing developed off the northwestern Bahamas in the 1930's. Both species of marlin are fished from a number of localities in the Bahamas throughout the year—white marlin being most abundant in spring, blue marlin in late spring and early summer. Sport fishing for marlins has been excellent off Havana, Cuba, in seasons similar to those in the Bahamas, but this activity has diminished in the past decade.

White and blue marlins are available throughout the Caribbean Sea, and sport fishing facilities have been developed in many localities. The oldest and most important center is the Venezuelan coast in the vicinity of La Guaira, where marlin fishing became popular soon after 1945. Fishing is excellent for white marlin in late summer and early fall, and for blue marlin in winter and spring. Fishing facilities for marlin also exist at many other localities, including the Virgin Islands, Puerto Rico, and Jamaica. Blue marlin usually are more abundant than white marlin off these islands. The best seasons usually are fall for small blue marlin, spring and early summer for large.

FIGURE 1.—The western North Atlantic Ocean, showing localities and areas of particular interest in the present study.

Marlin fishing in the Gulf of Mexico developed in the late 1950's off the Mississippi Delta, largely as a result of exploratory fishing catches of the Bureau of Commercial Fisheries vessel *Oregon*. The fishing season extends from early June into October, with a peak in July. In the late 1960's, a very productive area, centered on the De Soto Canyon in the northeastern Gulf, was fished from ports in western Florida and Alabama. This fishery also extends from June into October, but peaks in August. In 1969, some boats from Texas extended their operations farther offshore to the edge of the continental shelf and caught marlins consistently there for the first time.

Although most of the centers of sport fishing for marlin in the Atlantic are on the American coasts from Venezuela to Massachusetts, or on adjacent islands, there are several in other localities, such as Bermuda, the Azores, Rio de Janeiro in Brazil, and Cape Town in South Africa.

TAGGING STUDIES

METHODS

Cooperating fishermen marked white and blue marlins caught on rod and reel with dart tags as described by Mather (1963). Since this procedure does not require handling the fish or removing them from the water, their sizes were estimated. Tags and applicator poles were distributed to sportsmen by the Woods Hole Oceanographic Institution, either directly or through clubs and fishing tournament committees. Interest in tagging was stimulated by the press, radio, and television and also by clubs or tournament committees which offered incentives for tagging.

The tags carried the legend "reward" and the address of the Institution. (The fishermen often were more interested in receiving information on the tagged fish than in obtaining the $5 reward.) Posters were displayed where anglers gathered, and contact was maintained with fishery research agencies to which tags were apt to be returned. Some fishermen believed that the information gained from tagging hurt them and helped others. However, the volume of tagging and the percentage of returns increased over the years as more fishermen became aware of the program, and the mounting pressure by increased commercial fishing effort on the stocks demonstrated to fishermen the need for information on migratory patterns, population identity, and the effects of fishing.

WHITE MARLIN

A total of 6,590 white marlin were tagged and released in the western North Atlantic from 1954 through 1969; 65 tags have been returned as of June 1, 1970 (Table 1 and Appendix). Most releases (5,340) were made off the middle Atlantic coast of the United States from Cape Hatteras to Cape Cod. Other release sites were off southeastern Florida and the Bahamas, off Venezuela and in nearby waters, in the West Indies (Virgin Islands and Puerto Rico), in the northern Gulf of Mexico, and in the oceanic North Atlantic. Of the 65 tag recoveries, 41 were by commercial fishermen and 24 by sportsmen (Table 2). Before 1968, the Japanese longline fishery was the largest longline fishery in the Atlantic and covered nearly the entire ocean, but only 13 tags from white marlin have been returned from this

TABLE 1.—Releases (after slash) and returns (before slash) for white marlin tagged in the western North Atlantic Ocean by year and area of release.

Year	Area								Total	
	Hatteras to Chesapeake	Chesapeake to Barnegat	Barnegat to Cape Cod	Oceanic North Atlantic	SE Florida and W Bahamas	West Indies and vicinity	Gulf of Mexico	Venezuela and vicinity	Number	Percent
1954	--	--	0/4	--	--	--	--	--	0/4	0
1955	--	1/116	--	--	--	0/8	0/21	--	1/145	0.7
1956	--	1/402	--	--	--	0/3	0/8	--	1/413	0.2
1957	0/3	0/140	0/1	0/1	--	--	--	--	0/145	0
1958	0/1	0/39	0/1	--	--	--	--	--	0/41	0
1959	--	0/190	0/10	--	--	--	--	0/2	0/202	0
1960	--	0/96	0/2	--	0/4	0/1	0/4	0/4	0/111	0
1961	0/2	2/187	0/10	--	0/13	0/9	0/11	0/30	2/262	0.8
1962	0/30	4/294	0/18	--	0/41	--	0/4	--	4/387	1.0
1963	0/75	4/533	0/4	0/3	0/35	--	0/10	--	4/660	0.6
1964	4/182	8/258	0/1	0/5	1/67	--	0/13	--	13/526	2.5
1965	0/15	6/258	0/5	--	0/69	0/5	0/8	2/25	8/385	2.1
1966	1/36	7/172	1/64	0/6	1/54	0/4	0/23	1/149	11/508	2.2
1967	0/37	3/234	0/6	--	0/88	0/7	1/46	0/103	4/521	0.8
1968	1/100	8/569	0/32	--	0/94	0/16	0/56	0/16	9/883	1.0
1969	2/363	3/821	0/27	--	0/86	0/18	1/35	0/45	6/1,395	0.3
Unknown	1/1	1/1	--	--	--	--	--	--	2/2	
Total	9/845	48/4,310	1/185	0/15	2/551	0/71	2/239	3/374	65/6,590	

TABLE 2.—Returns from tagged white marlin, by fishery and nationality of recapturing vessel.

Type of fishery	Country	Number of returns
Sport fishery (rod and reel)	United States	24
Total		24
Commercial fishery (longline)	Canada	1
	Cuba[1]	14
	France	1
	Japan	13
	Norway	2
	South Korea	2
	United States	1
	Venezuela	7
Total		41
Grand total		65

[1] Some of the fish recaptured near Havana were caught by drift fishing from small boats with "criollo" lines. These usually consist of three interconnected lines with floats, each fishing at a different depth.

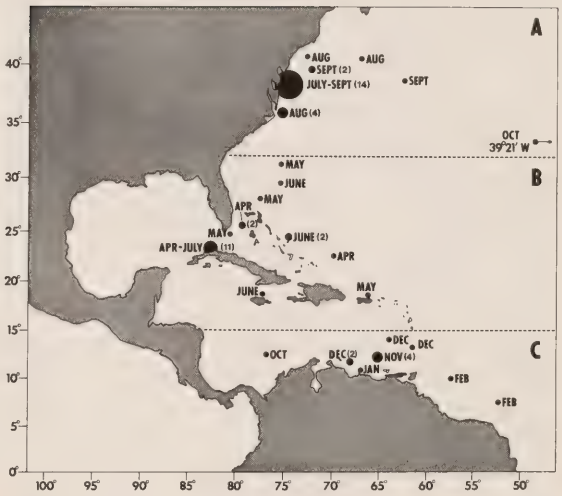

FIGURE 2.—Location of recaptures of white marlin tagged in the western North Atlantic Ocean north of lat 32°N between Cape Hatteras, N.C., and Cape Cod, Mass., in summer. The month of recapture is shown adjacent to each recapture site. The number of recaptures at each site is indicated by the number in parentheses (if more than 1) and by the size of the dot.

fishery. The Cuban and Venezuelan longline fisheries, though small compared to the Japanese fishery, accounted for 21 returns (14 and 7, respectively).

Tag recoveries from white marlin have been confined to the western North Atlantic. Of the 65 recoveries, 58 were from fish tagged off the middle Atlantic coast of the United States; we divided these into three groups on the basis of the area of recovery (Figure 2, Appendix):

Area A — North of lat 32°N
Area B — lat 15°N to lat 32° N
Area C — South of lat 15°N

In area A, 23 tagged marlin were recaptured in July through September and 1 in October; in area B, 22 were taken in April through July; and in area C, 12 were caught in October through February. The recaptures in the three areas are discussed below.

Area A

Of the 24 fish recaptured in area A, 14 were recaptured in coastal waters between Maryland and New Jersey. Twelve of these fish had been tagged locally (within 120 nautical miles of the point of recovery) and two had been tagged off Cape Hatteras. Of the fish tagged locally in July or August, three were recaptured in July or August of the same year; nine were recaptured in July or August of subsequent years. Time between tagging and recapture ranged from 9 days to 48 months. The 10 remaining fish tagged and recaptured in area A were recaptured in August, September, and October and at distances greater than 120 miles from the point of tagging. Some returns disclosed that in summer white marlin migrate along the east coast of the United States (Figure 3). Two fish tagged off Maryland and New Jersey were recaptured off North Carolina (150 and 200 miles distant) in 17 and 21 days, respectively. One white marlin traveled 500 miles, from off North Carolina to Georges Bank (off Cape Cod), in 12 days.

Two returns from considerable distances offshore showed that white marlin which range along the middle Atlantic coast in summer move offshore in the fall. One fish released off Maryland moved 580 miles eastward in 60 days, and the other, tagged in September 1966, was recaptured 25.3 months later at lat 33°15'N, long 39°21'W, about 1,800 miles east of Cape Hatteras.

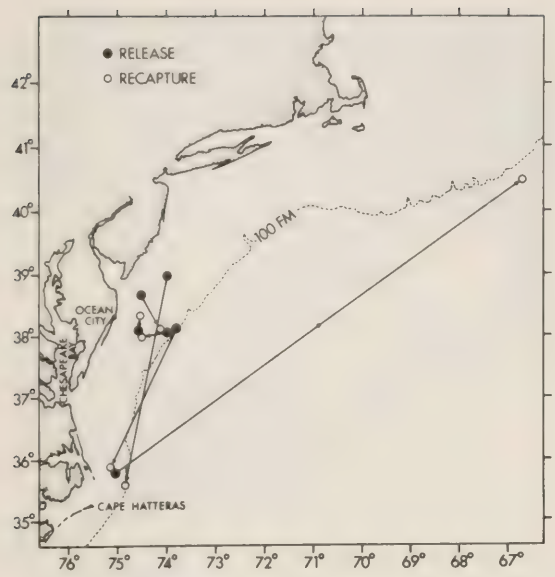

FIGURE 3.—Movements of tagged white marlin along the middle Atlantic coast of the United States, July-October. Recaptures were in the same year as releases.

Area B

Of the 22 white marlin recaptured in area B in April through July, 14 were taken in the Straits of Florida, 4 off the eastern Bahamas and eastern Greater Antilles, 3 were well off the southeast coast of the United States (between lat 28°N and lat 31°N), and 1 north of Jamaica.

Area C

Of the 12 tagged white marlin recaptured in area C, 1 was recovered in late October off Colombia, 9 were recovered in November, December, and January off Venezuela and the Lesser Antilles, and 2 in February off the Guianas.

The tagging results show clearly that white marlin in the western North Atlantic Ocean migrate seasonally. Fish tagged off the U.S. middle Atlantic coast apparently move offshore in late summer and fall from their summer grounds in coastal waters. They probably winter off the north coast of South America and move northward in spring back to the summer grounds. The large number of returns off Havana, Cuba, and the single return from north of Jamaica suggest that many move north through the Caribbean Sea and the Yucatan Channel. Four recoveries north of Puerto Rico and Hispaniola and east of the Bahamas indicate that white marlin also follow the Antilles Current[4] northward.

The nonrandom distribution of recoveries in areas A, B, and C reflects to some degree the seasonal nature of both the sport and commercial catches in those areas. In the Straits of Florida, however, tagged white marlin have been recaptured only in April through July even though the species is caught there throughout the year. Off the north coast of South America, white marlin are caught throughout the year by commercial and sport fishermen; yet tagged fish have been recaptured only in October through February.

The remaining 7 of the total of 65 returns were from 1,235 white marlin released from sport fishing centers in southeast Florida and the Bahamas (551 releases), the Gulf of Mexico (239), Venezuela (374), and the West Indies (71) (Table 1, Figure 4). Two white marlin tagged off Venezuela in August and September were recaptured after 3 to 4 months at large—one in November in the release area and the other in December off the coast of the Guianas. A third fish, tagged off Venezuela in October, was recaptured 20 months later (June) off South Carolina, probably en route to the U.S. middle Atlantic coastal region. Two white marlin tagged in the Bahamas were recaptured: one tagged in March was recaptured in June of the same year off St. Augustine, Fla., and the other, tagged in January, was recaptured in July in the Gulf of Mexico. Two white marlin tagged in July in the northern Gulf of Mexico were recaptured in the same area—one within a month and the other a year after tagging.

The two returns from off the eastern United States in June (from fish tagged in the Bahamas and off Venezuela) fit well with the indicated

[4] Names of currents are from Neumann and Pierson (1966).

FIGURE 4.—Location of releases and recaptures of white marlin tagged in the western North Atlantic Ocean south of lat 32°N. The months of release and recapture are shown in that order for each return. The number of recaptures at each site (if more than 1) is indicated in parentheses.

migratory pattern, but the remaining five do not. We do not now understand the relation between the nearly simultaneous summer and early fall concentrations of white marlin off the U.S. east coast and in the northern Gulf of Mexico. An interchange of fish between these two areas has not been demonstrated. None of the white marlin released in the Gulf of Mexico have been recaptured elsewhere, but a white marlin tagged in the Straits of Florida in January was recaptured in the Gulf of Mexico the following July. This recapture indicates that white marlin found off the northwestern Bahamas in winter may be a component of the summer concentration in the Gulf of Mexico. If this indication is correct, white marlin from the Bahamas could be migrating westward through the Straits of Florida while others en route to the U.S. middle Atlantic coast from the Caribbean are passing through the Straits to the east. White marlin are caught throughout the winter in the Bahamas, but fish tagged off Cape May-Cape Hatteras appear to migrate through the region only from early April to mid-July.

Tag returns indicate that white marlin off Venezuela in August and September remain off the north coast of South America into November and December, and that they are then joined by fish from the U.S. middle Atlantic coast. We are not sure how the marlin in the summer and early fall concentration off Venezuela are otherwise related to those in the summer and early fall concentrations in the Gulf of Mexico and off the U.S. middle Atlantic coast.

Early opinions that white marlin and other billfishes are short-lived and grow rapidly (Voss, 1956) are apparently true for Atlantic sailfish, *Istiophorus platypterus* (de Sylva, 1957), but de Sylva and Davis (1963) pointed out that white marlin may be long-lived. Their opinion was based on the weight-frequency distributions of fish in the U.S. sport fishery and the recovery of a tagged fish which had been at liberty for 4 years (Mather, 1960). The more recent information gained from tagging supports the belief of de Sylva and Davis (1963). Six tagged white marlin have been recaptured after 3 to 4 years at liberty. A comparison of sizes at release (estimated) and recapture does not indicate rapid growth after recruitment into the fishery.

We estimated the mortality rate of white marlin from tag-return data, using returns from white marlin tagged north of lat 32°N only (most fish were tagged in this area; those tagged in other areas might have had different migratory patterns). Moreover, we confined our consideration to returns from fish tagged in 1961 through 1965, because only two fish tagged before 1961 were recaptured and because returns from fish tagged after 1965 were incomplete. When the data were platted from white marlin recaptured from less than 1 month to more than 48 months after tagging, the recovery rates approximated an exponential relationship. The tag returns were grouped into time periods such as 0-12 months and 12-24 months, in view of a preliminary analysis which indicated that the returns within the first 6 months were in accord with the general pattern of returns

(Table 3, Figure 5). The indicated mortality rate was 27% per year, with 95 percent confidence limits of 14% and 39% (Z, the coefficient of instantaneous total mortality = 0.32 ± 0.17).

TABLE 3.—Summary of recaptures of tagged white marlin (to December 31, 1969). Dashed lines enclose data used for mortality estimates.

Year	Number tagged	Number recaptured[1]	Months at large				
			0-12	12-24	24-36	36-48	>48
1954	4						
1955	145	1					1
1956	413	1	1				
1957	145						
1958	41						
1959	202						
1960	111						
1961	262	2			1	1	
1962	387	4		2		2	
1963	660	4	2	1	1		
1964	526	12(13)	6(7)	2	3	1	
1965	385	6(8)	3(4)	2(3)	1		
1966	508	9(11)	4(6)	3	1	1	
1967	521	3(4)	1	(1)	2		
1968	883	9	6	3			
1969	1,395	5(6)	5(6)				
Unknown	2	2					
Total	6,590	58(65)	28(33)	13(15)	9	5	1
Total, 1961-65 only			11(13)	7(3)	6	4	

[1] Number recaptured are for groups A-C (see Appendix); numbers for groups A-D, if different, are shown in parentheses.

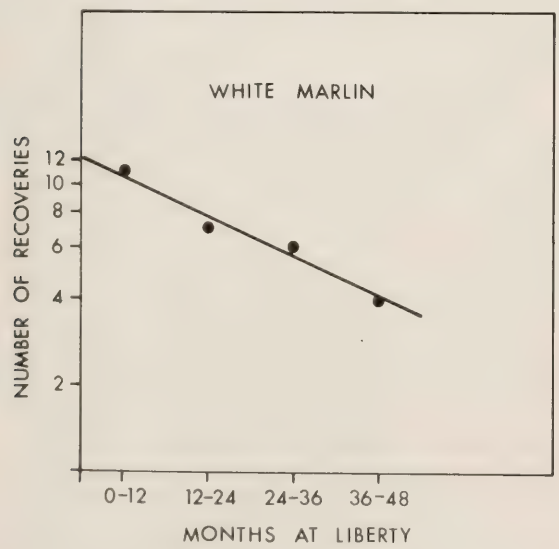

FIGURE 5.—Number of returns of white marlin tagged from 1961 to 1965 in waters north of lat 32°N, plotted by time at liberty.

BLUE MARLIN

Since 1954, 486 blue marlin have been tagged in the western North Atlantic; 3 have been recovered, all near their respective release points. One blue marlin released off Chub Cay, Bahamas, in August 1968, was recaptured off nearby Andros Island the following December; one released off La Guaira, Venezuela, in August 1966, was recaptured in the same area in October 1968; and one released off Biloxi, Miss., in June 1969, was recaptured 5 months later off Sabine Pass, La., 350 miles to the west. The returns indicate that meaningful information about blue marlin can be obtained if sufficient numbers are tagged.

LONGLINE CATCHES

METHODS

Data on the catch of marlins by the Japanese longline fishery in the Atlantic Ocean have been published by Shiohama, Myojin, and Sakamoto (1965) and by the Fisheries Agency of Japan (1966, 1967a, b, 1968, 1969). Catches of white and blue marlins, and those of other billfishes and tunas, are listed in those publications by 5°-quadrangles for each month, beginning in June 1956. Although catches in the categories "black marlin" and "striped marlin" also are listed, systematists do not presently recognize that black marlin, *Makaira indica*,[5] and striped marlin, *Tetrapturus audax*, occur in the Atlantic Ocean. We do not know whether those catches were misidentified or whether these species do, in fact, occur in the Atlantic. The catches listed in the two categories were too few to affect the conclusions of our study even if they were really white or blue marlin.

For each species, the catch per unit of effort (CUE), in fish per 100 hooks, was calculated for each 5°-quadrangle-month stratum in the period 1956-67 for which data were available. These CUE's were computed by dividing the number of fish caught in each such stratum by 1% of the number of hooks fished in it. To show seasonal distribution, average (unweighted)

[5] Ueyanagi et al. (1970) report occasional catches of *M. indica* in the equatorial and southeastern Atlantic.

CUE's for each 5°-quadrangle-month stratum were obtained by summing its yearly CUE's and dividing by the number of years.

The Japanese longline fishery in the Atlantic Ocean is directed primarily toward catching yellowfin tuna, *Thunnus albacares,* and albacore, *T. alalunga,* (Wise and Le Guen, 1969). Since marlins form only a small part (<3%) of the total catch of scombroid fishes, fishermen probably do not select specific fishing areas for marlins or adapt their fishing gear to catch marlins more effectively than other species. Possibly the catch rates for marlins are influenced by variations in the availability or the catchability of the fish, but the effects of such variations cannot be distinguished on the basis of the available data. We believe, therefore, that the catch rates by the longline fishery represent reasonably well the relative apparent abundance of marlins in the areas and seasons of intensive fishing. On this basis, we discuss distribution of white marlin and blue marlin in the Atlantic Ocean in the next sections.

WHITE MARLIN

The catches of the wide-ranging Japanese longline fishery show that white marlin are distributed over a much broader area than that indicated by returns from fish tagged in the sport fishery in the western North Atlantic Ocean. White marlin have been caught in all consistently fished areas of the Atlantic Ocean from lat 40°N to lat 40°S (Figure 6). The available data indicate that white marlin are scarce in both the north and south temperate zones in their respective winters (December-February and June-August).

Catch rates above 0.5 fish per 100 hooks are reported more often in the western than in the eastern Atlantic Ocean. We therefore conclude that although the distribution of white marlin is oceanwide, the species is more abundant in the western Atlantic. Sport fishermen report that white marlin are often concentrated at the edge of the continental shelf. Data from the longline fishery support this conclusion, inasmuch as the catch rates are generally higher in 5°-quadrangles adjacent to, or including, the edge of the shelf than in quadrangles in mid-ocean. No evidence has been found to date to suggest that the relative apparent abundance of white marlin in the Atlantic Ocean has been markedly affected by the longline fishery (Wise and Le Guen, 1969).

North Atlantic

In winter (December-February) white marlin are concentrated in the eastern Caribbean Sea and off the north coast of South America as far south as the equator. In spring some of these fish move northward into the Antilles Current beginning in March, and others move westward into the western Caribbean beginning in May and June. The northward movement of the first group conforms to the migrational pattern deduced previously from tag returns, but the second group appears to move into the northern and western Gulf of Mexico in summer, a pattern not supported by tagging data.

High catch rates in October, 300 to 1,200 miles off the east coast of the United States, support the hypothesis derived from tag returns —that white marlin summering off the U.S. mid-Atlantic coast move offshore in fall. In the Gulf of Mexico, however, white marlin are relatively abundant through October.

South Atlantic

In summer (December-February) white marlin are concentrated in the central South Atlantic Ocean and off the coast of Brazil. In the latter area, catch rates are among the highest known, occasionally reaching 3.8 white marlin per 100 hooks. In autumn (March-May) catch rates are generally lower than in summer and the marlin are not caught as far south. Because large areas of the South Atlantic are not fished in the autumn, catch rate data may not reflect a true picture of distribution. From June through September white marlin in the South Atlantic are concentrated in the South Equatorial Current and off the southwest coast of Africa. This season is the only one in which white marlin apparently are concentrated along the coast of Africa. From September through November,

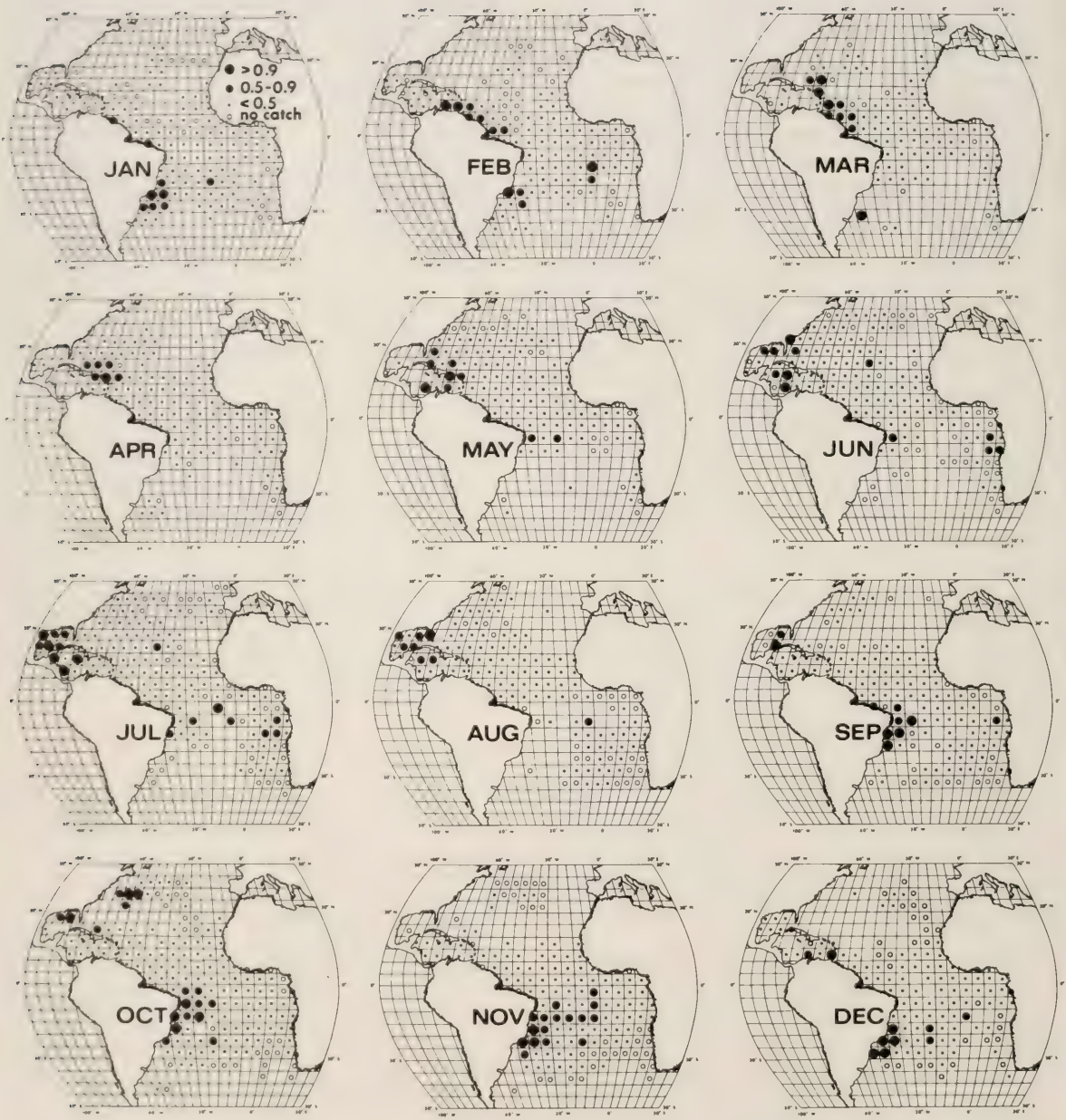

FIGURE 6.—Distribution and apparent relative abundance of white marlin in the Atlantic Ocean. Data are from records of the Japanese longline fishery, 1956-67. The catch per unit of effort (CUE) for each month in the rectangle is the arithmetic mean of the CUE of each month that the area in the rectangle was fished in the 12-year period. CUE is the number of fish caught per 100 hooks.

FIGURE 7.—Distribution and apparent relative abundance of blue marlin in the Atlantic Ocean. Data are from records of the Japanese longline fishery, 1956-1967. The catch per unit of effort (CUE) for each month in the rectangle is the arithmetic mean of the CUE of each month that the area in the rectangle was fished in the 12-year period. CUE is the number of fish caught per 100 hooks.

white marlin again are concentrated in the western South Atlantic off Brazil and in the South Equatorial Current.

We hypothesize that there are no major migrations of white marlin between the North and South Atlantic Oceans because the areas of concentrations of white marlin in the two oceans are generally separated by areas of low catch rates for white marlin and because not a single fish tagged in the North Atlantic has been recaptured in the South Atlantic. The North and South Atlantic groups of white marlin may be separate populations; Kamimura and Honma (1958a, b) believe that the closely related striped marlin of the Pacific Ocean has separate populations in the northern and southern hemispheres.

BLUE MARLIN

Monthly distribution of catches of blue marlin by Japanese longliners reveals two major seasonal concentrations in the Atlantic Ocean (Figure 7). In the Caribbean Sea, Gulf of Mexico, and the western North Atlantic Ocean south of lat 35°N, blue marlin are most abundant in the longline fishery from June through October. In the western and central South Atlantic Ocean, between lat 10° and lat 20°S, blue marlin are most abundant in February, March, and April. Possible migratory routes between the two areas are fished by the Japanese during all months of the year, but longline catches have produced no evidence that blue marlin move between the two oceanic regions. There may be two populations of blue marlin in the western Atlantic which are relatively unavailable to the longline fishery at certain seasons of the year, or there may be a single population which is unavailable to the fishery while the fish are migrating between the two areas. We believe that the two widely separated concentrations of blue marlin represent separate spawning populations. The evidence suggests that blue marlin in the North Atlantic spawn mainly from July through September and those in the South Atlantic spawn in February and March. It is unlikely that a single population of blue marlin would spawn at two widely separate locations at different times of the year. Eschmeyer and Bullis (1968) examined four larvae of blue marlin from the western North Atlantic captured in July and September, and Gehringer (1957) reported three larvae from the western North Atlantic and Gulf of Mexico in spring and summer, which were later identified as blue marlin by Ueyanagi and Yabe (1959). Caldwell (1962) reported on two postlarvae of blue marlin captured off Jamaica in September. Erdman (1968) concluded from his studies of gonad development and sex ratio that the peak spawning season for blue marlin off Puerto Rico was in July and August. In the South Atlantic, Bartlett and Haedrich (1968) reported on 85 larvae of blue marlin captured off the coast of Brazil in February and March. The size range was from 4.9 to 32.0 mm.

The blue marlin is apparently the only[6] billfish in the Atlantic whose abundance has been significantly affected by longline fishing. Wise and Le Guen (1969) showed significant rates of decline in relative apparent abundance of blue marlin in the two areas of major concentrations shown in Figure 7. They stated that these declines were associated with the intensive fishing for albacore and yellowfin tuna in the same areas. Ueyanagi et al. (1970) also reported a drastic decline in the apparent abundance of blue marlin in the Atlantic with the level of apparent abundance in 1965 only about one-fourth of that of 1962.

SUMMARY

WHITE MARLIN

1. Tag returns indicate that one group of white marlin moves from the middle Atlantic coast of the United States in summer to the north coast of South America in winter. The route appears to be initially offshore from the summer grounds, then south to the wintering area. The return is north in the vicinity of the Antilles and the Bahamas, including the Yucatan Channel and the Straits of Florida.

2. Longline catches support the above hypothesis but also indicate that a second group of

[6] Recent unpublished data suggest that the abundance of broadbill swordfish and white marlin in the Atlantic may also have been reduced by longline fishing.

white marlin moves from the wintering area off the coast of South America to summer grounds in the Gulf of Mexico. The relation between these two groups, which have different summering areas but similar wintering areas, is not clear, nor is their relation to a third group of white marlin which summers off Venezuela.

3. White marlin in the South Atlantic are separate from those in the North Atlantic and migrate from the eastern South Atlantic in winter to the western South Atlantic in summer.

4. White marlin appear to be relatively long-lived. An annual mortality of 27% was estimated from tag return data.

BLUE MARLIN

1. Only three tag returns have been recorded for blue marlin; all were relatively near the points of release.

2. Analysis of Japanese longline catch records for blue marlin reveals concentrations during summer and early autumn on the western side of the North and South Atlantic Oceans. In winter these concentrations disperse, and no pattern of distribution is apparent.

3. The two populations appear to be separate. We believe that spawning takes place in spring and summer for each group.

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The tagging results were made possible by the thousands of anglers, captains, and mates who have tagged and released many of their catches, and the clubs and tournament committees which have encouraged tagging. We regret that space does not permit individual acknowledgments here; the major participants are listed in the informal progress reports on the Cooperative Game Fish Tagging Program which are issued periodically by the WHOI. The press and the broadcasting media have also done much to encourage tagging and the return of tags.

[7] National Sea Grant Program, National Oceanic and Atmospheric Administration, Department of Commerce.

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APPENDIX

Release and recapture data for white marlin tagged in the western North Atlantic Ocean, 1954-69, are given in four Appendix Tables. Tagged fish are grouped by areas of release and recapture in order of recapture date. Data in parentheses were estimated by anglers at time of tagging. Although anglers estimated lengths in inches and weights in pounds, we have converted them to metric units.

APPENDIX TABLE 1.—Group A: White marlin tagged and recaptured north of lat 32°N.

Release data					Recapture data							Months at liberty
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	*kg*				*cm*	*kg*			
July 11, 1955	(38°10′	74°45′)	(220)		July 18, 1959	37°31′	74°44′		(25.0)	RR	U.S.	48.2
July 31, 1962	(38°10′	74°45′)	(200)		Aug. 18, 1963	38°07′	74°52′	234	29.0	RR	U.S.	12.6
Aug. 7, 1961	37°53′	74°42′		(20)	Aug. 7, 1964	35°47′	75°05′	201	21.8	RR	U.S.	36.0
July 17, 1963	37°48′	74°41′		(12)	Aug. 9, 1964	(38°10′	74°45′)			RR	U.S.	12.8
July 30, 1964	35°47′	75°05′	(230)		Aug. 11, 1964	40°31′	66°45′		(16.8)	LL	Can.	0.4
July 27, 1964	(38°10′	74°45′)		(27)	Aug. 26, 1964	38°20′	74°38′			RR	U.S.	1.0
July 12, 1964	(38°10′	74°45′)		(18)	Sept. 10, 1964	38°40′	62°10′		(18.2)	LL	Jap.	2.0
July 28, 1962	37°50′	74°57′	(200)		Aug. 15, 1965	38°04′	74°47′	218		RR	U.S.	36.6
Aug. 7, 1965	38°42′	74°32′		(36)	Aug. 16, 1965	38°10′	74°10′	195	24	LL	Nor.	0.3
Aug. 2, 1964	36°05′	75°12′	(200)		Aug. 25, 1965	38°38′	74°25′	221	30.4	RR	U.S.	12.8
Aug. 26, 1963	(38°10′	74°45′)		(27)	Sept. 16, 1965	39°40′	72°20′			LL	Nor.	24.7
July 23, 1965	(38°51′	74°30′)	(200)		Aug. 4, 1966	40°45′	72°21′	226	30.4	RR	U.S.	12.4
July 17, 1966	38°58′	74°00′		(20)	Aug. 7, 1966	35°28′	74°52′	208	18.2	RR	U.S.	0.7
Aug. 24, 1964	(38°10′	74°45′)		(14)	Aug. 14, 1966	39°07′	74°25′	193	16.8	RR	U.S.	23.7
Aug. 18, 1964	36°00′	74°56′	(210)		Sept. 10, 1966	37°58′	74°55′	213	22.7	RR	U.S.	24.6
July 12, 1965	37°50′	74°57′	(210)	(18)	Sept. 13, 1966	39°31′	71°40′		31.8	LL	U.S.	14.1
July 9, 1968	(38°11′	74°00′)		(45)	Aug. 17, 1968	38°02′	74°35′	208	20.4	RR	U.S.	1.3
Sept. 13, 1966	38°30′	73°30′		(24)	Oct. 22, 1968	33°15′	39°21′	180		LL	S.K.	25.3
July 22, 1968	38°15′	73°50′	(220)		July 18, 1969	37°56′	74°40′	221	29.4	RR	U.S.	11.8
July 22, 1968	38°15′	73°50′		(20)	Aug. 4, 1969	38°15′	73°50′			RR	U.S.	12.4
Aug. 11, 1968	38°42′	74°25′		(18)	Aug. 6, 1969	36°12′	75°00′	(211)	(20.4)	RR	U.S.	11.8
July 21, 1968	37°26′	75°06′	(210)	(27)	Aug. 7, 1969	38°04′	74°10′	211	25.0	RR	U.S.	12.6
Aug. 13, 1969	38°13′	73°51′		(18)	Aug. 30, 1969	35°52′	75°12′	(203)	(25.0)	RR	U.S.	0.6
July 14, 1967	38°10′	74°32′		(23)	Aug. 31, 1969	37°31′	74°22′		(21.3)	RR	U.S.	25.6

[1] RR, rod and reel; LL, longline; CL, criollo line.

APPENDIX TABLE 2.—Group B: White marlin tagged north of lat 32°N and recaptured between lat 15°N and lat 32°N.

Release data					Recapture data							Months at liberty
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	*kg*				*cm*	*kg*			
(Summer 1956)	(38°10′	74°45′)			Apr. 30, 1957	23°12′	82°05′		27.2	CL	Cuba	
Aug. 26, 1962	37°40′	74°54′	(210)		Apr. 8, 1964	23°11′	82°23′	218	25.0		Cuba	19.4
Sept. 6, 1961	38°14′	73°53′			May 5, 1964	23°14′	82°20′				Cuba	32.0
Aug. 29, 1963	38°02′	74°04′			May 8, 1964	23°13′	82°22′		22.7	CL	Cuba	8.3
Aug. 19, 1964	(38°10′	74°45′)			June 14, 1965	29°32′	75°13′			LL	Jap.	9.8
Aug. 1, 1964	38°30′	73°30′	(180)		June 27, 1965	24°23′	74°04′	(120)		LL	Jap.	10.9
Aug. 17, 1964	37°51′	74°58′		(18)	July 2, 1965	23°17′	82°21′		22.7		Cuba	10.5
July 1965	38°22′	74°30′		(36)	Apr. 2, 1966	25°42′	79°21′	234	40.9	RR	U.S.	(8.6)
(Aug. 1962)	(38°10′	74°45′)			Apr. , 1966	25°42′	79°21′		25.0	RR	U.S.	(43)
July 23, 1965	37°56′	74°40′		(32)	June 14, 1966	(23°15′	82°17′)		18.2		Cuba	10.7
July 21, 1966	(38°10′	74°45′)		(32)	May 5, 1967	31°10′	75°10′	220	30	LL	Cuba	9.5
July 4, 1966	38°30′	73°30′	(160)	(18)	May 28, 1967	23°05′	83°13′	200	25.0	CL	Cuba	10.8
Aug. 12, 1966	(39°18′	74°00′)		(20)	May 10, 1968	(23°05′	82°45′)	213	25.0	CL	Cuba	20.8
Aug. 9, 1966	40°52′	71°44′		(40)	May 18, 1968	18°38′	66°07′	234	40.9	RR	U.S.	21.2
July 17, 1965	38°09′	74°30′		(25)	June 20, 1968	23°14′	82°22′		35.8	CL	Cuba	35.1
Sept. 3, 1966	35°49′	74°56′	(200)		July 11, 1968	23°14′	81°55′	228	15.9	LL	Cuba	22.2
Aug. 18, 1964	38°47′	74°17′	(200)		July 20, 1968	23°10′	82°30′		15.0	CL	Cuba	47.0
Sept. 24, 1968	38°22′	73°41′		(27)	Apr. 27, 1969	22°40′	69°50′		23	LL	S.K.	7.0
Sept. 17, 1967	38°15′	73°50′			(May 15, 1969)	28°06′	77°16′		15	LL	Cuba	(20.5)
July 25, 1967	38°44′	74°29′	(230)	(27)	May 31, 1969	24°49′	80°29′	206	19.1	RR	U.S.	22.2
July 13, 1968	38°00′	74°00′		(18)	June 7, 1969	24°30′	74°40′	180	22.5	LL	Jap.	10.8
Aug. 23, 1968	35°47′	74°40′	(190)	(19)	June 21, 1969	18°45′	77°04′	170	20.0	LL	Jap.	9.9

[1] RR, rod and reel; LL, longline; CL, criollo line.

APPENDIX TABLE 3.—Group C: White marlin tagged north of lat 32°N and recaptured south of lat 15°N.

Release data					Recapture data							Months at liberty
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	*kg*				*cm*	*kg*			
Aug. 8, 1963	38°50′	74°30′			Dec. 10, 1963	13°15′	61°30′		18.2	LL	Fr.	4.1
Aug. 20, 1964	35°50′	75°00′	(200)	(20)	Dec. 12, 1966	12°05′	67°55′		25.0	LL	Ven.	27.8
July 27, 1966	37°58′	74°38′		(18)	Jan. 2, 1967	10°55′	67°00′			LL	Ven.	5.2
Aug. 31, 1964	37°47′	74°49°		(17)	Feb. 15, 1967	07°25′	52°20′			LL	Ven.	29.5
Unknown	(36°00′	75°00′)			Nov. 8, 1968	12°30′	65°25′					
(Aug. 1, 1968)	38°15′	73°50′			Feb. 13, 1969	10°02′	57°22′	157	20.5	LL	Ven.	(6.6)
Aug. 4, 1969	36°12′	75°12′		(28)	Oct. 29, 1969	12°40′	76°53′		25			2.8
Aug. 12, 1969	(38°15′	73°50′)		(23)	Nov. 13, 1969	12°07′	64°50′		(17)	LL	Jap.	3.1
Unknown	(38°15′	73°50′)			Nov. 25, 1969	11°58′	65°14′		(20)	LL	Jap.	
July 24, 1966	37°59′	74°44′		(27)	Nov. 28, 1969	11°58′	65°14′		(20)	LL	Jap.	39.2
Aug. 18, 1969	(35°57′	75°01′)	(200)	(18)	Dec. 14, 1969	14°00′	64°00′	140	(15)	LL	Jap.	3.9
July 18, 1969	37°54′	74°36′		(20)	Dec. 16, 1969	11°25′	68°12′		(17)	LL	Jap.	5.0

[1] RR, rod and reel; LL, longline; CL, criollo line.

APPENDIX TABLE 4.—Group D: White marlin tagged south of lat 32°N.

Release data					Recapture data							Months at liberty
Date	Locality		Estimated size		Date	Locality		Size		Gear[1]	Flag	
	Lat N	Long W	Length	Weight		Lat N	Long W	Length	Weight			
			cm	*kg*				*cm*	*kg*			
Jan. 18, 1964	25°43′	79°20′		(23)	July 25, 1964	23°37′	92°37′		2.2	LL	Jap.	6.2
Aug. 21, 1965	(10°50′	66°55′)		(30)	Dec. 28, 1965	09°15′	57°50′	250	14.2	LL	Jap.	4.2
Mar. 24, 1966	(25°20′	77°58′)		(18)	June 3, 1966	29°35′	76°50′	210	20	LL	Jap.	2.3
Sept. 4, 1966	10°47′	66°57′		(20)	Nov. 25, 1966	10°55′	67°00′	160	22	LL	Ven.	2.7
Oct. 16, 1965	(10°50′	66°55′)		(25)	June 14, 1967	32°27′	76°00′	193	16	LL	Cuba	19.9
July 3, 1967	29°55′	86°46′	(210)	(27)	July 31, 1968	29°49′	87°17′	234		RR	U.S.	12.9
July 31, 1969	29°55′	87°05′	(200)	(20)	Aug. 13, 1969	29°51′	86°48′	201	25.0	RR	U.S.	0.4

[1] RR, rod and reel; LL, longline; CL, criollo line.

RETENTION OF LARVAL HERRING WITHIN THE SHEEPSCOT ESTUARY OF MAINE

JOSEPH J. GRAHAM[1]

ABSTRACT

This paper demonstrates a system of larval movements that retains larval herring within an estuary despite its seaward residual flow. Data are reviewed from a 2^3 factorial design using buoyed and anchored nets in a narrow channel of the estuary. Three factors were involved: location, tidal phase, and depth. Catch rates of larvae relative to these factors suggested that the larvae maintained their position in the upper portion of the estuary by (1) occupying the landward net tidal flow near the bottom, (2) moving upward upon reaching the limit of their landward penetration (3) then seaward in the net flow near the surface, and (4) finally descending again into the landward net flow.

Larval herring, *Clupea harengus harengus* Linnaeus, move up the Sheepscot estuary of Maine primarily in the autumn and spring. During these seasons the larvae accumulate in the upper portion of the lower estuary where they are retained despite the residual seaward flow of the estuary. Statistically significant differences in the distribution of larval herring according to depth and location and the interaction of these two factors with tide suggested that the larvae were using tidal flows to migrate (Graham and Davis, 1971). This paper examines the data, upon which the statistical results were based, to demonstrate a system of larval movements that retain the larvae within the estuary.

MATERIALS AND METHODS

Buoyed and anchored nets were fished (Figure 1); their construction and validity in sampling larval herring is noted briefly in this paper and is available in detail in another paper (Graham and Venno 1968). Four nets were attached to one line which was buoyed at the surface and anchored to the bottom to sample at predetermined depths (0, 10, 15, and 20 m). A flow meter measured the amount of water strained, from its central position in the mouth of each net. The mouth opening of the net was 0.5 m in diameter and the length of the net was 1.9 m. Mesh diameter was 0.75 mm. Filtration efficiencies of the net ranged from 80 to 90% at current speeds above 15 cm/sec and 100% within speeds from 15 to 3 cm/sec. Below 3 cm/sec the impeller of the flow meter does not revolve. Tests simulating sampling conditions showed that clogging did not change these filtration efficiencies.

The nets fished approximately 6 hr on the flood and 6 hr on the semidiurnal ebb tides. They were set at slack water during dusk, retrieved and reset at the end of the tidal stage during slack water. Two lines of nets were set at the landward end of the estuarine channel and two were set at the seaward end (Figure 2). The sampling area within the estuarine channel was 9 km long, 275 m wide, and about 20 m deep throughout its length. The distance between sets at the seaward end of the channel was 2 km, that between the landward sets was 3.2 km, and the distance between the two locations was 3.8 km as measured from the interior sets.

For a given line of nets catch rates were determined for the two nets above mid-depth and for the two nets below mid-depth. In each case, the total amount of water strained for the two nets above and below mid-depth was

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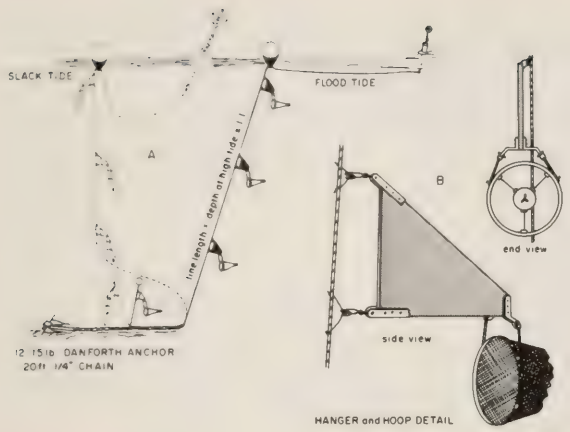

FIGURE 1.—Buoyed nets for sampling larval herring. A, positions of four nets during slack and flowing tides; B, arrangement of hanger and hoop (After Graham and Venno, 1968).

divided into the total number of larvae captured and multiplied by 100 to obtain catches per 100 m^3. Thus, at each location (landward and seaward) average catch rates from the two lines of nets were obtained for two depths (shallow and deep) during two tidal stages (flood and ebb), providing eight samples for each location or 16 samples for a single overnight experiment.

The nets were fished during darkness because the larvae avoided the nets during daylight. A comparison of nighttime catches between two lines of buoyed nets set in tandem within the channel and a comparison between nighttime catches of buoyed nets with those of a high speed Boothbay Depressor Trawl (Graham, Chenoweth, and Davis, 1972) suggested that the larvae did not avoid the net at night nor did they escape from the nets during slack water. The average catches above and below mid-depth determined the concentration of larvae in the water layers above and below the level of no-net-motion of the tidal flows. Larvae in the upper layer would experience a net seaward transport and those in the lower layer would experience a net landward transport. In addition to sampling larvae already in the channel, the two lines of nets in the landward location would sample larvae transported into the channel by the ebb tide and the

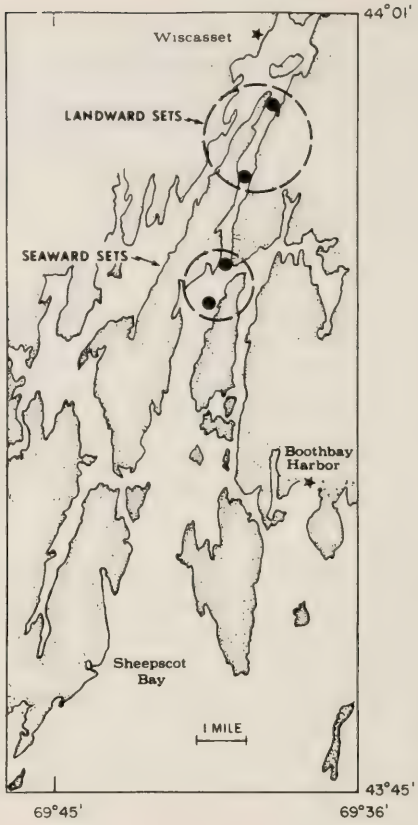

FIGURE 2.—Locations (circled) of buoyed and anchored nets in the Sheepscot estuary of Maine (after Graham and Davis, 1971).

two lines in the seaward location would sample larvae transported into the channel by the flood tide.

The arrangement of the nets and catches in the estuarine channel constituted a factorial sampling design. A factorial design is especially adaptable to examining the effects of a number of different factors which vary in a regular way during an experiment. The source of regularity in the experiments was the tidal currents transporting the larvae. An example of the statistical procedures is given in Table 1. Catch rates were transformed into common logarithms to obtain a normal distribution of the data for computations. In this paper the untransformed catch

TABLE 1.—Statistical procedures for a 2^3 factorial design using larval catches per 100 m^3 of water strained from an experiment during Nov. 8, 1967. I) Factors are coded, II) Catches are assigned to the factorial order, III) the sums of squares are determined, IV) they are applied to an analysis of variance, and V) a conclusion is determined from the analysis.

I. *Factors and their codes (A).*

Tidal phase	(A)	flood	(+)	ebb	(−)
Water depth	(B)	shallow	(+)	deep	(−)
Location	(C)	landward	(+)	seaward	(−)

II. *Factorial order (1) of larval catches per 100 m^3.*

		Seaward location		Landward location	
Flood	Shallow	5.44(4)	9.78(4)	2.64(8)	5.54(8)
	Deep	11.53(2)	3.51(2)	86.09(6)	48.60(6)
		Seaward location		Landward location	
Ebb	Shallow	2.89(3)	6.29(3)	33.28(7)	24.73(7)
	Deep	0.44(1)	4.73(1)	26.75(5)	4.58(5)

III. *Determination of the sums of squares for the 2^3 factorial design using logarithms of the catches; 1 has been added to each characteristic.*

Factorial order		A	B	AB	C	AC	BC	ABC
(1) 0.6435	1.6749	−	−	+	−	+	+	−
(2) 2.0618	1.5453	+	−	−	−	−	+	+
(3) 1.4609	1.7987	−	+	−	−	+	−	+
(4) 1.7356	1.9903	+	+	+	−	−	−	−
(5) 2.4273	1.6609	−	−	+	+	−	−	+
(6) 2.9350	2.6866	+	−	−	+	+	−	−
(7) 2.5221	2.3932	−	+	−	+	−	+	−
(8) 1.4216	1.7435	+	+	+	+	+	+	+
Total =		+1.5382	−0.5694	−4.1060	+4.8792	−1.9718	−2.6984	−2.4612
Sums of squares (Total) $\frac{2}{16}$ =		0.1479	0.0203	1.0537	1.4879	0.2430	0.4521	0.3786

IV. *Analysis of variance.*

Factor	Sum of squares	Degrees of freedom	Variance	*F*-ratio
A	0.1479	1	0.1479	1.04
B	0.0203	1	0.0203	0.14
AB	1.0537	1	1.0537	7.40*
C	1.4879	1	1.4879	10.45*
AC	0.2430	1	0.2430	1.71
BC	0.4521	1	0.4521	3.17
ABC	0.3786	1	0.3786	2.66
Within	1.1394	8	0.1424	
Total	4.9229	15		

*Statistically significant, $P_{.05} = 5.32$

V. *Conclusion.*

Significantly more larvae were captured below mid-depth (deep) on the flood tide and more above mid-depth (shallow) on the ebb tide. In addition, significantly more larvae occurred at the landward location than at the seaward location.

rates are used because they are more familiar than logarithms as measures of concentrations of larval fishes in their environment. The results of the statistical analysis are given by Graham and Davis (1971). Significant differences between catch rates with depth and location and the interaction of these two factors with tide occurred primarily in the autumn and spring. Of eight experiments conducted from late October to early December (1965-67) five had significant differences between larval catch rates. Of 10 experiments completed between mid-March and mid-May (1966-68) six had significant differences between catch rates. The distributions of larvae from experiments that had significant differences in larval catch rates will be described, and an explanation for the absence of significance in the other experiments will be discussed.

RESULTS AND DISCUSSION

Concentrations of larval herring were evident within the channel when the distributions of catch rates that differed statistically within the

experiments were examined. The analysis of variance from an experiment on November 8, 1967 (Table 1, IV) showed that the catch rates of larvae differed significantly with location and with the interaction of depth and tide. The untransformed catch rates showed that concentrations of larvae were shallow during the ebb tide and deep during the flood tide. Also, more larvae occurred at the landward end of the channel than at the seaward end. These data and those from other experiments having significantly different distributions in catch were summarized in Table 2. For example, the interaction on November 8 was illustrated by first summing all of the cubic meters of water strained by the shallow nets and then all of the larvae captured by them. These totals were used to obtain an average catch per 100 m^3 of water strained; the process was repeated for the deep nets. Beginning anew, the average catch rates were determined for the two locations. The numbers in parentheses in Table 2 locate the concentrations of larvae within the channel diagrammed in Figure 3. Those concentrations of larvae captured in the shallow nets had a net transport seaward during an experiment and those in the deep nets were transported landward. A transition in such transport occurred for those larvae concentrated throughout the water column at one location or the other. The arrows in Figure 3 infer a system of movements from the location and transport of the larvae that appears analogous to those of other larval fishes (Pearcy and Richards, 1962) and planktonic organisms (Bousfield, 1955) which are retained in estuaries by tidal currents. The suggested movements

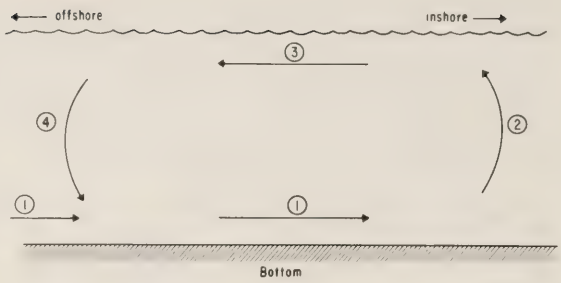

FIGURE 3.—Diagram of a system of larval movements thought to retain larval herring in the Sheepscot estuary. The numbered distributional components of the system coincide with the numbered catches in Table 2.

TABLE 2.—Catch rates from 11 experiments in the autumn and spring. The distributions of rates for single factors and for two factors (interaction X) are given. Numbers in parentheses are from Figure 3; unnumbered catch rates are discussed in the text.

Single factor—depth

	Dec. 7, 1967	*Mar. 20, 1967*	*May 4, 1967*
Shallow	1.95(3)	0.62	40.64(3)
Deep	0.60	7.15(1)	7.66

Single factor—location

	Nov. 8, 1967	*Nov. 21, 1966*	*Dec. 7, 1967*	*Mar. 14, 1968*
Landward	29.56(2)	20.76(2)	1.84(2)	6.16(2)
Seaward	6.60	11.43	1.26	2.06

Two factor—depth × tide

	Flood	*Ebb*	*Flood*	*Ebb*	*Flood*	*Ebb*
	Nov. 1, 1965		*Nov. 8, 1967*		*Nov. 21, 1966*	
Shallow	4.20	11.12(3)	6.11	18.57(3)	3.84	15.46(3)
	×		×		×	
Deep	10.40(1)	1.43	48.42(1)	18.17	34.85(1)	8.96
	Dec. 6, 1966		*Apr. 27, 1966*		*May 9, 1967*	
Shallow	10.08	4.03	16.74	14.53	18.80	4.40
	×		×		×	
Deep	1.48	7.94	8.74	20.84	2.78	12.10

Two factor—location × tide

	Flood	*Ebb*	*Flood*	*Ebb*
	Mar. 26, 1966		*Apr. 26, 1966*	
Landward	3.41	11.46(2)	16.98	15.28
	×		×	
Seaward	10.54(4)	1.66	9.32	27.27

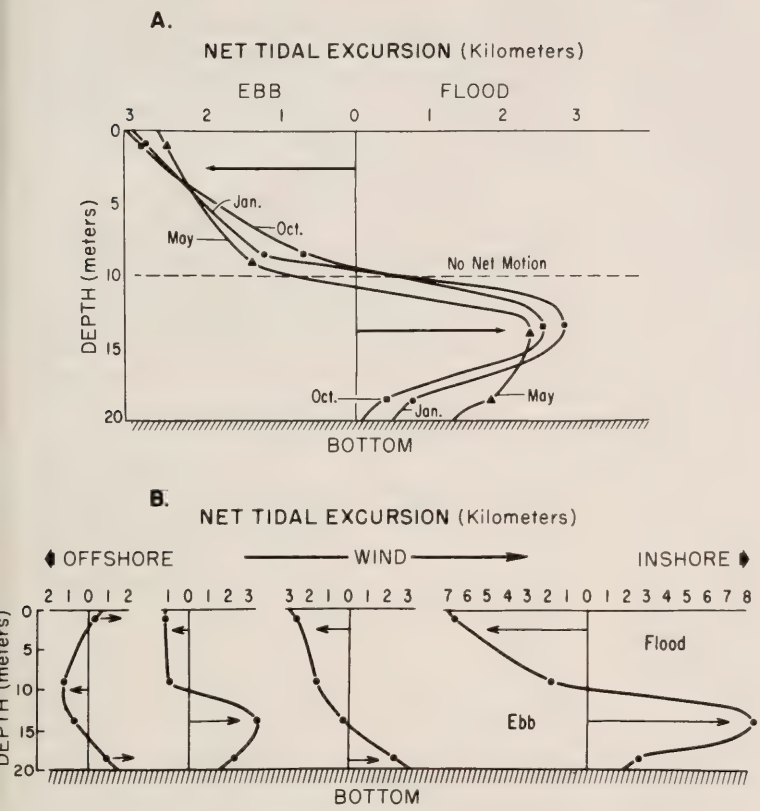

FIGURE 4.—A. Vertical profiles of mean tidal excursion for the four sets of buoyed nets in the estuary of the Sheepscot River (after Graham and Davis, 1971). B. An effect of onshore wind on the net tidal excursions for individual sets of nets in the estuary.

would retain the larvae within the channel after they had entered it on the net flood tide near the bottom.

The system of movements diagrammed in Figure 3 is based on the average two-layer semidiurnal tidal flow (Figure 4A). But the dynamics of estuarine flow can be changed by large amounts of freshwater discharge, wind direction and velocity, and the shape of the channel. Graham and Venno (1968) found that an increase in freshwater discharge and the shape of the channel could change considerably the catch of buoyed nets in the Sheepscot estuary. Although the nets were positioned in the experimental design to lessen such effects, three of the experiments had results that could not be attributed to the system of movements; they are unnumbered in Table 2. All three had interactions between depth and tide and in one case (April 27, 1966) between location and tide as well. The distribution of larval catches was opposite to that expected. For instance, catch rates were larger on the flood tide near the surface and on the ebb tide near the bottom. Because tide was involved in each case possibly these data resulted from unusual tidal dynamics. On May 9, 1967, tidal excursions were modified by winds. Winds blew landward and up the channel during the day preceding the setting of the nets and continued through the flood tide on the night the nets were set. Wind velocities were usually 10 to 20 knots with gusts up to 30 knots. Readings from flow meters showed a typically shaped profile of net tidal excursion at the most landward station (Figure 4B). This was progressively altered seaward until the last station

had a small net upstream flow at the surface. Apparently, the winds reversed the tidal flow to some extent and thus the larval distribution as well.

Although I cannot account with certainty for the system of larval movements in the sampling area, the most reasonable explanation is that the larvae responded to changes in the character of the tidal flow. Larvae are transported up the estuary at about 1.8 knots per semidiurnal tidal cycle (Graham and Davis, 1971) which approaches the average length of tidal excursions recorded at 15 m, below the level of no-net-motion. This level of no-net-motion is obliterated in the upper estuary where the maximum depth is 10 m and the channel widens and extensive mud flats are present. The transition zone between the lower and upper estuaries is near the town of Wiscasset (Figure 2) and coincides with the maximum shoreward penetration of an abundance of larvae. Stickney (1959) states that the upper estuary compared to the lower has a greater exchange ratio, lower and more variable salinity and a wider range in temperature. A reversing tidal falls 3.5 km above the transition zone completely mixes the water. The most likely agency to initiate the ascending response (Figure 3, No. 2) by the larvae would be the change in the character of the tidal flows caused by shoaling of the bottom rather than agencies peculiar to the estuary. Herring are retained throughout their larval life over the banks and ledges of the open waters of the Gulf of Maine where the water is shallow and the tidal flows are well developed but conditions are not estuarine. After a brief transport downstream near the surface the larvae would resume their usual transport by descending towards the bottom.

The results suggested that the arrangement of buoyed and anchored nets in the estuarine channel was appropriate to sampling larval herring transported within the tidal currents. Larvae were sampled efficiently on both the flood and ebb tides, since no important main effect was obtained for tidal phase during the experiments. To obtain such an effect would have required a larval concentration to pass beyond the positions of the nets; then the larvae would either have to miss the nets on the return tidal current or drift to some area in the channel where they were not subject to the currents. Because the larvae were transported by the tidal currents, tide was always one of the interacting factors and an interaction between depth and location was not obtained.

One explanation for the appropriateness of the sampling design was that concentrations of the larvae were of sufficient length to overlap a pair of nets when transported into a given location. When this occurred, the difference in catch rates between the two lines of nets within the location would be small, and the difference between the two lines of nets in the other location where the concentration did not occur would also be small. These differences within the locations provided a measure of experimental error in the sampling design and if small they would yield a statistically significant F-ratio when compared to differences in catch rates between location and depth and the interaction of these two factors with tidal phase (e.g., F = mean square between locations/mean square within locations). Statistical significance would not occur when a concentration overlapped only one line of nets in a given location; the differences in catch rates between the two lines of nets would be relatively large, as indicated for the exterior and interior nets of the seaward location in Table 3.

Although net tidal flows in the channel affected the transport of the larvae, temporal variations in tidal currents made it difficult to determine the exact nature of that transport. The catch rates and corresponding tidal excursions obtained from the nets were accumulative and

TABLE 3.—Larval catches per 100 m^3 of water strained from an experiment during March 28, 1968. When treated as in Table 1 the distributions of the catch rates were not statistically significant.

Tide	Depth	Seaward location		Landward location	
Flood	Shallow	2.35	7.74	4.46	4.32
	Deep	2.68	2.84	3.85	3.65
Ebb	Shallow	1.37	6.07	3.38	3.58
	Deep	1.40	11.09	3.79	5.87

did not represent the many changes that probably occurred in tidal currents with time. These currents change not only their velocity but their type of flow as well (Graham and Venno, 1968).

ACKNOWLEDGMENT

I am indebted to Bruce C. Bickford who operated the buoyed and anchored nets in the channel, sometimes during severe weather.

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ABUNDANCE, DISTRIBUTION, MOVEMENTS, AND LENGTHS OF LARVAL HERRING ALONG THE WESTERN COAST OF THE GULF OF MAINE

JOSEPH J. GRAHAM, STANLEY B. CHENOWETH, AND CLARENCE W. DAVIS[1]

ABSTRACT

This paper describes the abundance, distribution, movements, and lengths of larval herring along the western coast of the Gulf of Maine. Larvae were most numerous in the catches throughout the coast in the autumn, reached a low in the winter, and increased in the spring. Growth in the autumn is estimated at 1 to 1.3 mm per 5-day intervals. Larval mortality was highest in the autumn, lower in the winter, and lowest in the spring. The mortality in the winter usually varied with their condition and determined the subsequent level of spring abundance. We selected three different types of estimates as desirable for predicting the recruitment of immature herring to the sardine fishery of Maine: (1) winter mortality, (2) larval condition in the winter, and (3) spring abundance.

The commercial catch of 2-year-old Atlantic herring, *Clupea harengus harengus* Linnaeus, fluctuates annually along the western coast of the Gulf of Maine. The Maine sardine industry processes these immature herring, but cannot anticipate the amount of fish available for canning each year. One approach to this problem is to determine whether the abundance of herring during their first year of life is related to the number of fish entering the fishery. To establish whether such a relationship exists, the desirable estimate of abundance or its correlative must be determined first. We describe the distribution, abundance, movements, and lengths of larval herring along the western coast of the Gulf of Maine. We discuss the seasonal changes in larval abundance caused by their mortality and the relation of the sources of larvae to their distribution and movements. From these analyses we selected three types of estimates: (1) winter mortality, (2) larval condition in the winter, and (3) spring abundance.

Larval herring occur throughout the Gulf of Maine-Georges Bank area. They concentrate in the offshore bank area (Tibbo et al., 1958); along the southeastern coast of Nova Scotia (Das, 1968)[2]; and the western coast of the Gulf of Maine (Graham and Boyar, 1965). During their relatively long larval period, herring may drift with the residual currents about the banks and in the Gulf (Colton and Temple, 1961; Das, 1968, see footnote 2). Racial studies show that these larval herring have three parental stocks; namely, Georges Bank, the southern coast of Nova Scotia, and the western coast of the Gulf of Maine (Anthony and Boyar, 1968; Ridgway, Lewis, and Sherburne, 1969). The relation between the parental stocks and the larvae is not clear.

In the Boothbay area of the Maine coast, herring were found in estuaries and embayments throughout their larval life (Graham and Boyar, 1965). In this area larval catches reached a peak in the autumn shortly after hatching and declined to a minimum during winter. Catches were sporadic in the spring and in May the fish metamorphosed. Evidence that in the spring the larger larvae avoided our conventional sampling gear (Gulf III and meter nets) led to the development of the Boothbay Depressor trawl (Graham and Vaughan, 1966) and buoyed and

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[2] Das, N. 1968. Spawning, distribution, survival, and growth of larval herring (*Clupea harengus* L.) in relation to hydrographic conditions in the Bay of Fundy. Fish. Res. Board Can., Tech. Rep. 88, 129 p.

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anchored tidal nets (Graham and Venno, 1968). Catches with this gear provided information on mortality in an estuary (Graham and Davis, 1971), condition (Chenoweth, 1970), and seasonal feeding (Sherman and Honey, 1971). Coastal salinity, temperature, and currents were measured during zooplankton surveys (Sherman, 1970) and hydrographic surveys (Graham, 1970a, b).

MATERIALS AND METHODS

Larval herring were sampled in two areas (Figure 1): A coastal area which extended from the headlands to 20 km offshore (50-fm isobath) along the coast from Cape Ann, Mass., to Machias Bay, Maine; and the Boothbay area which extended to 6.5 km offshore (lat 43°45'N) and was bounded by the Sheepscot and Damariscotta estuaries. Collections were made once or twice each season in the coastal area from autumn 1962 through spring 1967; and every other week in the Boothbay area from autumn 1964 through spring 1967. Additional collections, obtained after 1967, will be cited when pertinent. There were 21 stations in the coastal area until the spring of 1965 when the number was increased to 46 to provide more adequate data. In autumn 1966, the area was divided into 30-min squares of latitude and longitude and the squares subdivided into quarters. The 46 quarters sampled on a given cruise were selected randomly. An exploratory winter cruise (1964) was made within the coastal bays and estuaries and two cruises were made in the Boothbay area in early March of 1964 and 1965. In the Boothbay area, samples were obtained in all locations that were navigable for the 13-m vessel, MV *Phalarope*.

Larval herring were collected by the methods listed in Table 1. We captured small larvae in the autumn with a Gulf III sampler (Gehringer and Aron, 1968) and larger larvae in the winter and spring with Boothbay Depressor trawls (Graham and Vaughan, 1966). Catches ob-

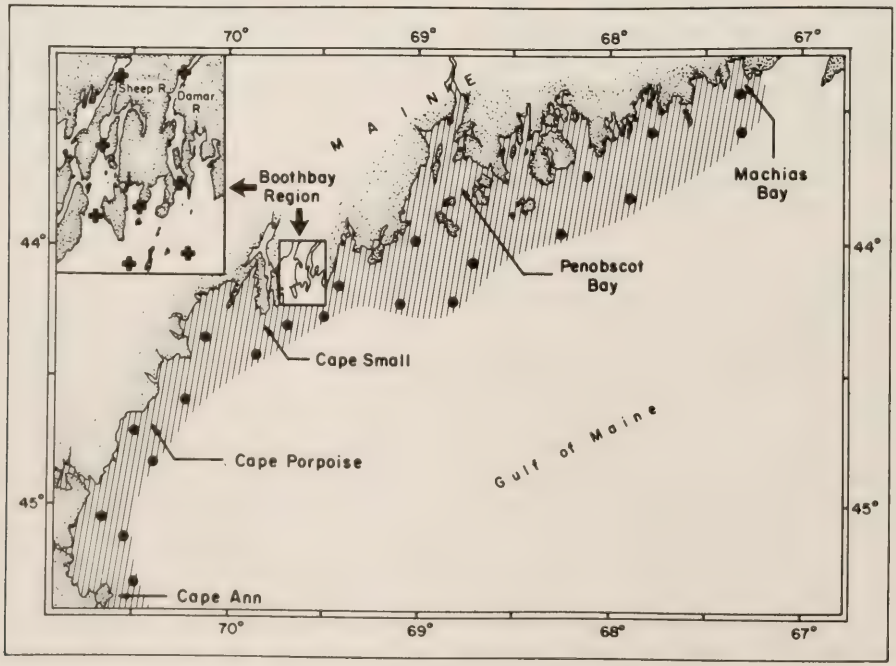

FIGURE 1.—The coastal (hatched) and Boothbay (enclosed) sampling areas along the western coast of the Gulf of Maine. Dots and crosses are station positions; S and D indicate the Sheepscot and Damariscotta estuaries.

TABLE 1.—Methods of sampling larval herring in the western Gulf of Maine, 1962-67. Volume sampled in 7½-min tow = given volume ÷ 4.

Area	Stations	Season	Gear type	Tow		Water strained	Towing velocity
				Depth	Duration		
				m	*min*	m^3	*knots*
Coastal	21-48	Autumn	Gulf III	0-10-20	30	200	6
		Winter-spring	Boothbay Depressor trawl				
			No. 1	0-10-20	30 (or 7½)	4,200 (1,050)	6
			No. 2	0-10-20	30	17,000	4½
			No. 4	0-10-20	30 (or 7½)	8,000 (2,000)	5
Inshore	8	Autumn	Gulf III	0-mid-depth-bottom	30	135	4½
		Winter-spring	Boothbay Depressor trawl				
			No. 1	0-mid-depth-bottom	30	[1]2,800-4,200	4

[1] Dependent on mouth opening of liner.

tained were adjusted to the number of larvae captured per 100 m^3 of water strained during a tow. During the coastal cruises the gear was towed obliquely for 30 min at each station (10 min each at the surface, at 10 m, and at 20 m) except on the coastal cruises after autumn 1966, when each of the 46 quarters was sampled with two oblique 7½-min tows (2½ min at the surface, at 10 m, and at 20 m). The direction of these two tows was selected randomly and catches were averaged to obtain an estimate of abundance. Filtration efficiencies of the sampling gear approached 100%. Comparisons between catch rates of the Gulf III and the Boothbay Depressor trawl differed on individual stations during tests covering the period of their exchange within the sampling program. However, the catch rates were similar for the two gear when they were averaged for stations or for an entire cruise. Experiments also showed differences in catch rates between short and long tows, between tows of different depths, and between tows made during nighttime and daytime. Only the differences between rates during nighttime and daytime were sufficiently important to the analyses of this report and they are given. Information on the length and depth of tow and comparisons of catch rates between the two gear are being prepared for publication.

Larval herring, preserved in 10% Formalin, were measured from the tip of the jaw to the end of the caudal peduncle (standard length). Conversion of this measurement (SL) extended to total length (tip of jaw to the tip of the longest lobe of the caudal fin) (TL) may be made for larvae from 20 to 45 mm SL by:

$$TL = -3.47 + 1.24\ SL$$

RESULTS

HATCHING

Catches of recently hatched herring (4-9 mm) provide evidence that there are several spawning areas along the western coast of the Gulf of Maine, but that the time of hatching differs between the eastern and western sectors of the coast. Recently hatched larvae were captured throughout the coastal sampling area from late September until early November. Some of these larvae had yolk sacs, especially those obtained near the headlands of the Boothbay area, where the occurrence of hatching was monitored each year. Relatively large numbers of larvae were captured east of Cape Small in the early autumn and to the west of this Cape in late autumn (Table 2). The autumnal hatch along the coast was expected, since Boyar (1968) found that the gonads of most adult coastal herring reached spawning condition by late September in this area. Also Goode (1884) and Bigelow and Welsh

TABLE 2.—Coastal distribution of the number of recently hatched larval herring from late September to mid-October and from then to early November; water tempertaures are from mid-October.

Area (Figure 1)	Percentage of larvae, 4-9 mm		Mean temperature (°C) mid-October 1963	
	Sept.-Oct. 1962-63 (N = 267)	Oct.-Nov. 1962-66 (N = 1,872)	Surface	Bottom
Cape Ann-Cape Small	9	97	12	8
Cape Small-Penobscot Bay	54	2	11	9
Penobscot Bay-Machias Bay	37	1	9	10

(1925) reported that herring spawned in the western area later than in the eastern sector of the coast. Hatching of larvae in the spring was observed only once; three larvae (8-9 mm) were captured in the Boothbay area in May.

The earlier hatching in the eastern sector of the coast may be attributed to the distribution of water temperature. The average surface temperature from 1963 through 1965 was 9.1°C in the western sector of the coast and 6.2°C in the eastern sector. Bottom temperatures during the same period averaged 4.5°C in the western sector and 5.6°C in the eastern. Each year the surface water was 2° to 3.5°C warmer in the western than in the eastern sector, while the eastern bottom water was 1° to 1.5°C warmer than in the western sector. These temperature trends were established primarily in the summer (Graham, 1970a) and persisted into the autumn (Table 2). Possibly, cooler autumn surface temperatures in the eastern sector would initiate spawning sooner than in the western sector; warmer bottom temperatures would incubate the eggs faster (Das, 1968, see footnote 2).

SEASONAL ABUNDANCE, DISTRIBUTION AND MOVEMENTS

Larvae were most numerous in the catches throughout the coast in the autumn, reached a low in the winter, and increased slightly in the spring (Figure 2). Catches were largest in the eastern sector of the coast in early autumn, but larger in the western sector by mid-autumn. By late autumn, catches dropped drastically in both sectors and reached a common level throughout the coast. In the Boothbay area the numbers of

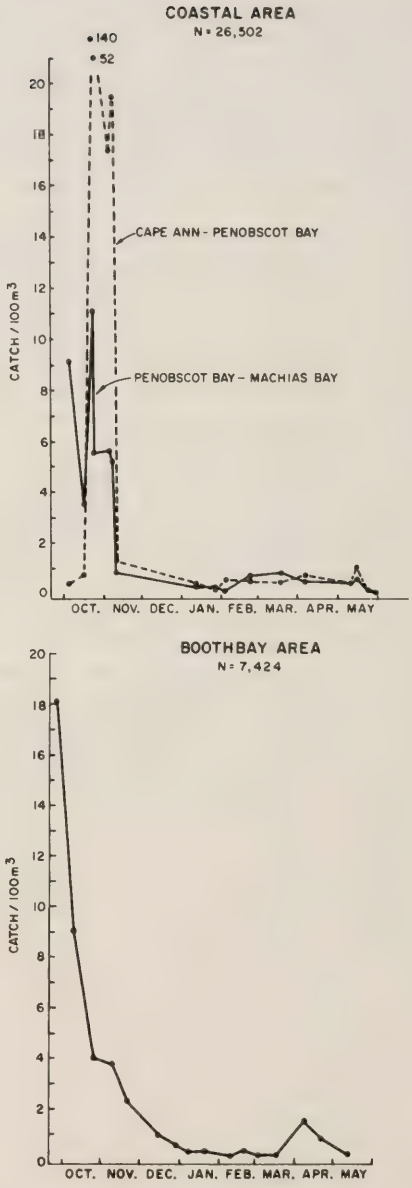

FIGURE 2.—Upper panel - mean catch rates of larval herring in the western (Cape Ann-Penobscot Bay) and eastern (Penobscot Bay-Machias Bay) sectors of the coast during cruises from 1962-67. Lower panel - mean catch rates from the Boothbay area for semimonthly periods combined for the years 1964-67. Points are plotted at the midpoint of the cruise periods.

captured larvae were also highest in the autumn, lowest in the winter with an increase in the spring. The timing of autumnal abundance varied between years and will be discussed in detail in the section on movements. As recorded by Graham and Boyar (1965) the Sheepscot estuary usually contained more larvae than the Damariscotta estuary. About 60-68% of the total catch was taken in the Sheepscot in a given year.

Seasonal changes in the dispersal of larvae were analogous to those of abundance. Larvae were aggregated in the autumn and spring and dispersed in the winter. For instance, catches during an autumn cruise had a coefficient of variation of 214%, during a winter cruise 17%, and during a spring cruise, 50%. Exploratory cruises showed that larvae were dispersed from the headlands to 28 km up the estuaries in the Boothbay area during early March when winter conditions still prevailed.

Changes in distribution occurred in the autumn and spring when the larvae moved landward. These changes were apparent when the average catch rates from the Boothbay area ($\bar{x}$ Boothbay) were compared synoptically with those from cruises in the adjacent coastal area from Cape Small to Penobscot Bay ($\bar{x}$ coastal). The synoptic catch rate from the Boothbay area was obtained by interpolating between rates of the biweekly cruises that occurred a few days before and after a given coastal cruise. The percentage catch rate of larvae in the Boothbay area [$\bar{x}$ Boothbay/$\bar{x}$ Boothbay + $\bar{x}$ coastal)] × 100 did not exceed 40% during October when hatching was at its peak, then reached almost 90% in November coincident with a decline in hatching (Figure 3). The percentage was again low in February and March, but increased to about 85% in April and May prior to metamorphosis. Similar comparisons between Boothbay data and those from coastal areas east and west of Boothbay did not yield these relations. Apparently, the shoreward shift in distribution was not synchronized along the entire coast.

Other movements of larvae were evident from an analysis of the data from the coastal and Boothbay areas. In autumn, an alongshore movement from east to west was apparent when

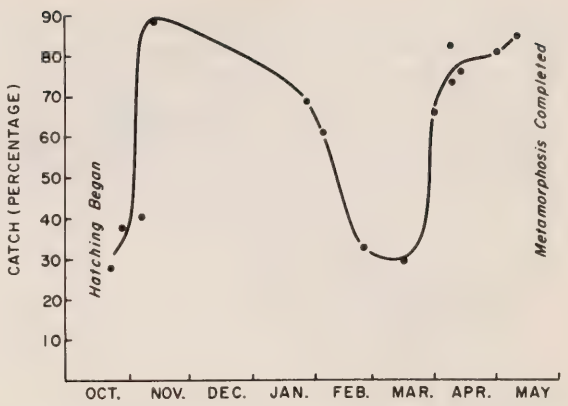

FIGURE 3.—The change in percentage in the average catch rate in the Boothbay area as compared with the average catch rate in the coastal area.

larvae were obtained in the Boothbay area that were larger than those recently hatched in the western coastal sector. The movement of larvae in the spring was marked by their accumulations in locations receiving shoreward intrusions of coastal water and by the relation of their distribution with that of surface salinity. The intrusions resulted from eddies formed by the spacing of river discharge along the western sector of the coast (feathered arrows, Figure 4). The configurations of isohalines and lines of equal larval density throughout the coast were often similar. Such similarity indicated that the magnitude of station-to-station differences in catch paralleled the station-to-station differences in salinity. These differences were accumulated for coastal stations from west to east and their frequency distributions were plotted on probability paper for two cruises having widely different salinity distributions (Figure 5). The cumulative frequencies of salinity and catch were alike for a given cruise, but differed between cruises. We infer from these results that the larvae are carried by currents, indicated by the station-to-station differences in salinity. The precise direction of drift cannot be ascertained because it is not possible to determine whether the salinity distribution is causing the current or is the effect of the current, perhaps generated by winds.

FIGURE 4.—(a) Isohalines (‰) during a spring cruise, March 28-April 13, 1967. Feathered arrows indicate shoreward intrusions of coastal water (from Graham, 1970b), and unfeathered arrows indicate current directions along the coast (from Bumpus and Lauzier, 1965). (b) Isolines of larval catch rates (no/100 m^3) for the above cruise.

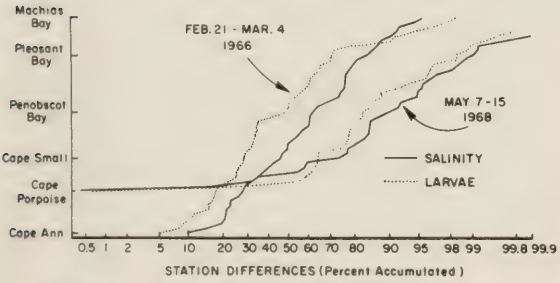

FIGURE 5.—Accumulated frequency distributions of station-to-station differences from west to east along the coast. The cruise in 1968 began to the east of that in 1966.

Larval movements up the estuaries during autumn were easier to detect in the Boothbay area because larvae were transported inshore primarily by tidal flows (Graham and Davis, 1971). Tidal flows followed the inshore-offshore axes of the estuaries and embayments; thus the landward movement was detected by grouping catches made at the three outer estuarine, three lower estuarine, and two upper estuarine stations, and plotting them in a time series. Peaks in larval abundance progressed from outer to upper estuarine stations with time, suggesting an inshore movement of the larvae (A, B, and C in Figure 6). Two such progressions were obtained in 1966 and one in both 1964 and 1965. In 1964, larvae passed the outer and lower stations between our scheduled cruises and appeared first at the upper stations as a peak in abundance in early October. In spring, larvae were always more abundant at the upper estuarine stations, and progressions in peaks of abundance up the estuary were not apparent.

LARVAL LENGTHS

The rate of increase in average length varied seasonally and geographically. Data from the coastal and Boothbay areas showed a marked

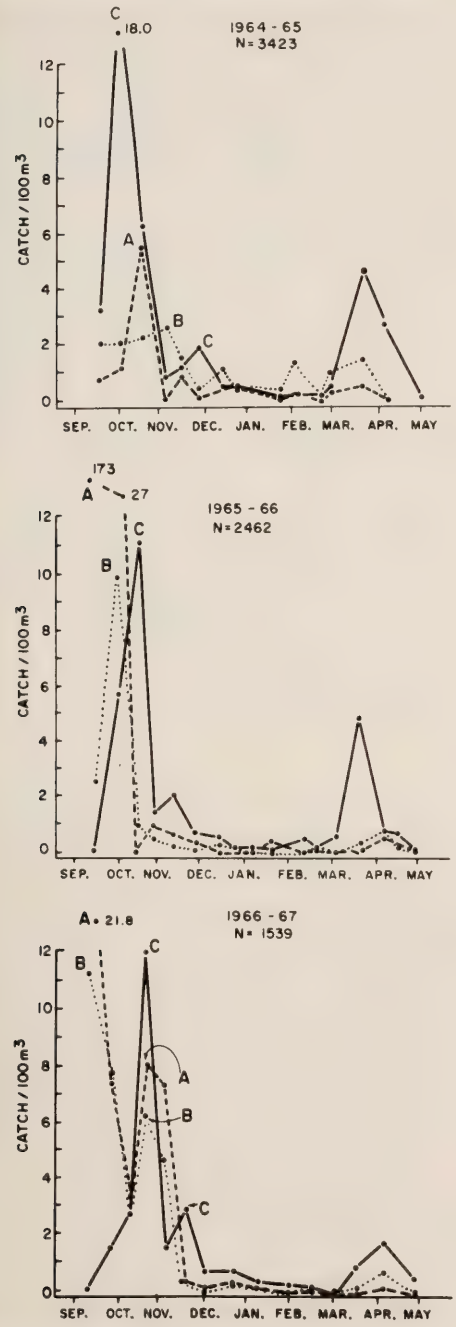

FIGURE 6.—Seasonal changes in larval abundance in the Boothbay area during 1964-67. Values are plotted for outer (A), lower (B), and upper estuarine (C) stations.

increase in length in the autumn followed by a more gradual increase in the winter and spring (Figure 7). During the autumn and spring the increase in length accompanied a comparable increase in weight, but not in the winter when the larvae were very thin (Chenoweth, 1970). In the coastal area the increase in length

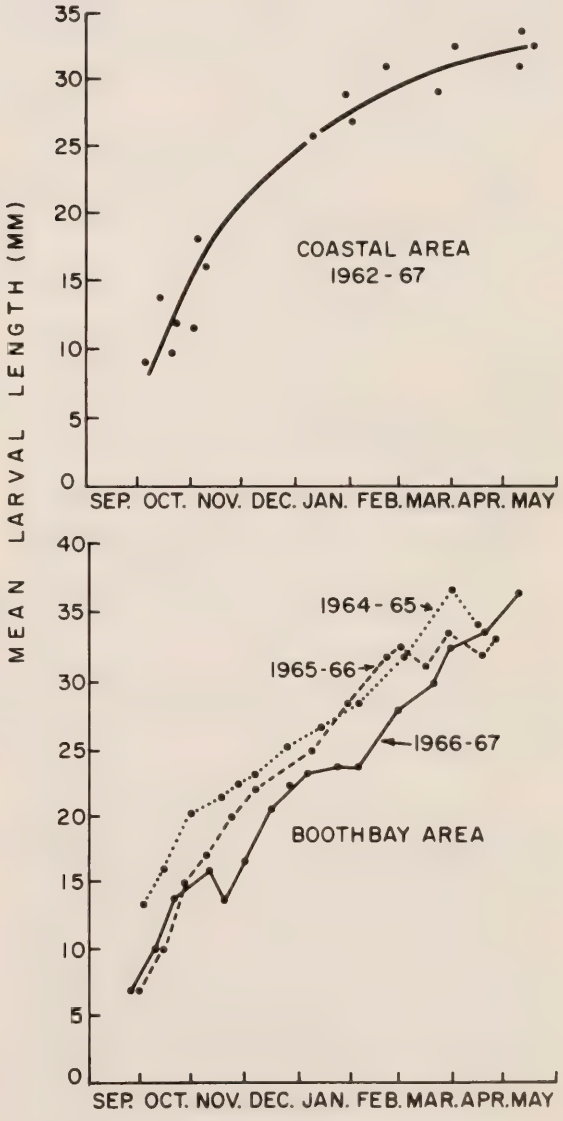

FIGURE 7.—Seasonal change of mean larval length in the Boothbay and coastal areas, 1962-67.

appeared asymptotic while the average length fluctuated above and below 32 mm in the Boothbay area from March through May in 1965 and 1966. Differences in the average length also occurred between the eastern and western sectors of the coast. In late September to mid-October, the mean lengths did not differ greatly along the coast (Figure 8). By early November the mean length was larger in the eastern sector than in the western sector, but this difference diminished in winter; by spring mean lengths were similar along the coast.

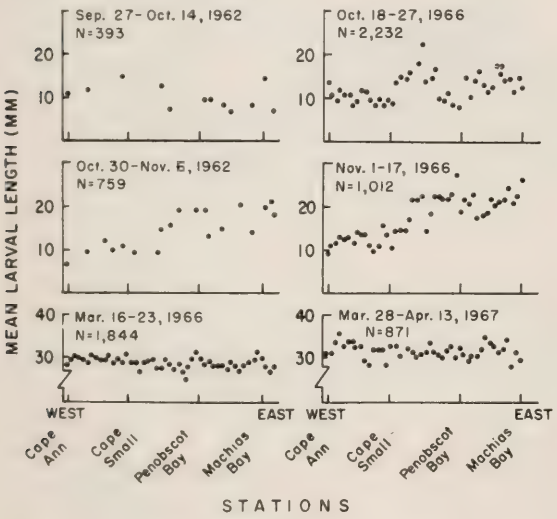

FIGURE 8.—Variations in the average length of larval herring from west to east along western coast of the Gulf of Maine.

The seasonal change in mean length (Figure 7) was influenced by the movements of larvae, their avoidance of our sampling gear, and their departure from the vicinity of our sampling stations after metamorphosis. Broods of larval herring moved shoreward in the autumn from the coastal water, but the size at which they initially entered the Boothbay area varied. This is illustrated by data from 1964 and 1965; data from 1966 were similar to those of 1965. In autumn 1964, two broods of larvae (labeled a and b in Figure 9) initially entered the Boothbay area; the more abundant had a size mode of 13 mm, the other was recently hatched and had a size mode of 9 mm. By mid-October these two broods were of equal abundance. In November a third brood (c) was detected, during a coastal cruise, that had a modal length of 13 mm, equal to the modal length of larvae initially entering the Boothbay area. Presumably, the addition of this group in part slowed the shift in modal length to only 3 mm from mid-November to late December. These variations in size resulted from the location of the Boothbay area within an east-west coastal zone of transition for hatching time. Also, some of the larvae hatched in the eastern sector of the coast at an earlier time and were carried westward along the prevailing currents (Graham, 1970b) and then into the Boothbay area.

In autumn 1965, a single brood (d) of recently hatched larvae with a modal length of 7 mm initially entered the area. In October, this brood was still the most important contributor to the inshore area, since the modal size from a coastal cruise in October coincided with the seasonal progression of larval size within the Boothbay area. A second group (e) of recently hatched larvae entered the area in early November.

In the spring it was obvious that we were failing to catch the larger larvae and the spring peak in catch rates should have been considerably larger than that recorded for daytime tows. We assumed that this failure was due to their avoidance of our gear because we captured more of these larger larvae at night when they could not see the gear. Day and night cruises were alternated in the Boothbay area from January through April during 1965 and 1966. The size ranges of larvae captured during these cruises were the same, but the modal length was much larger for larvae captured during the night cruises. The length-frequency curves for all larvae from the day and night cruises showed two distinct modes, one at 33 mm and the other at 40 mm (Figure 10). At 36 mm the percentages of larvae in the day and night catches were identical. For larvae larger than 36 mm the percentages increased for night catches and decreased for day catches, indicating that avoidance increased progressively until the larvae grew to 40 mm. Initial nighttime catches of

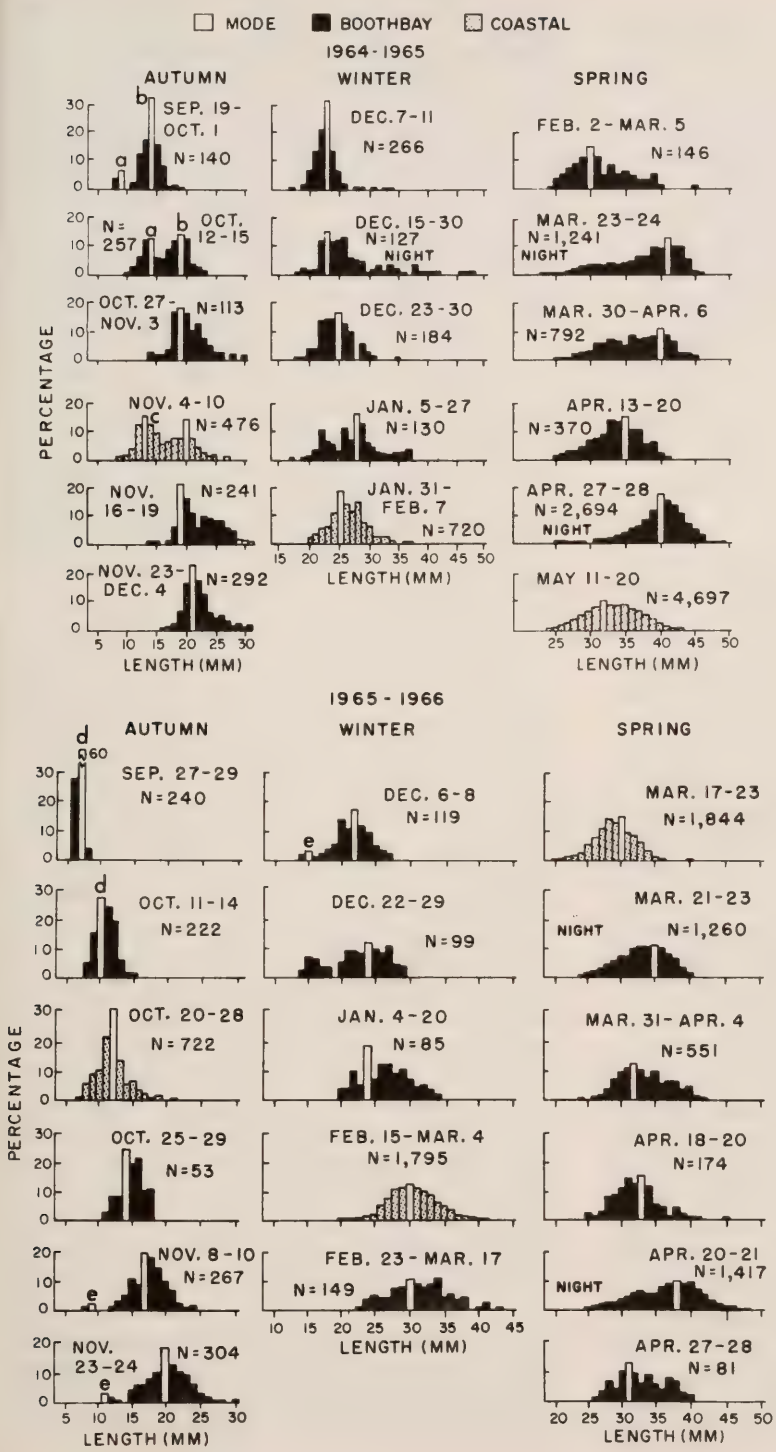

FIGURE 9.—Size distribution of larval herring during 1964-66. Only the most obvious modal lengths are indicated for the data from the Boothbay and coastal areas and those modes discussed in the text are labeled a to e.

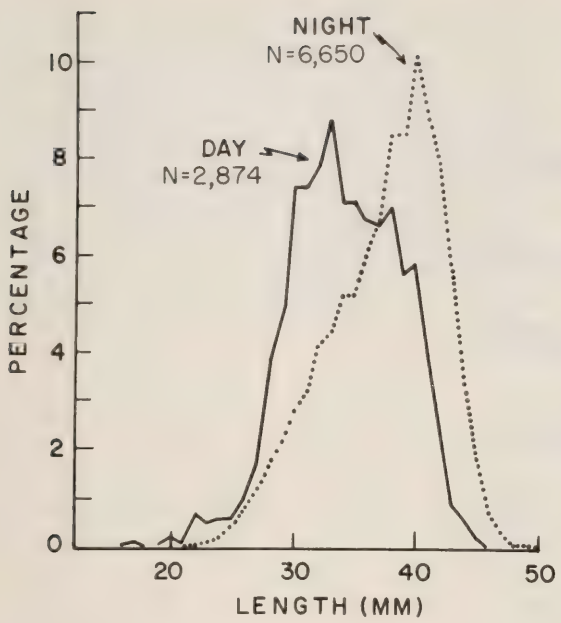

FIGURE 10.—Length-frequency curves of larvae captured in the Boothbay area at night and during the day.

those larvae larger than 36 mm occurred earlier in the year and their peak in abundance occurred later than that of larvae captured during the day (Figure 11). In 1964, losses by avoidance began in December. Failure to catch larvae began later the following year (in January) because the larvae that initially entered the Boothbay area were smaller than those that entered in 1964 (Figure 7). Catches of larvae larger than 36 mm in length in the Boothbay area were similar to those obtained with buoyed and anchored nets set in the Sheepscot estuary at night during 1966. This similarity indicated the ease with which larvae were captured at night. The buoyed nets strain water at a much lower velocity than the trawl.

In late April larvae were occasionally observed schooled in shallow coves. By late May large numbers of these fish were frequently observed in the shallow coves whereas the numbers captured at our sampling stations had declined. This change in distribution was coincident with the period of metamorphosis (about 41-50 mm SL) from larval to juvenile form. Metamorphosed herring were found in the Boothbay and other inshore areas but not in the outer coastal waters during the summer (Davis and Graham, 1970).

Variations in the lengths of larvae in our samples related to their shoreward movements, avoidance of gear, and departure from our sampling stations, caused discrepancies when estimating the real growth of larvae in their environment. Some estimate of growth rate may be obtained, however, from changes in modal length at certain times of the year. During 1965, the modal lengths of a single abundant group of larvae may be traced from the autumn into December. This group was not greatly influenced by mixing with other groups of different sizes and avoidance of our gear was not yet important. From late September to early December, the

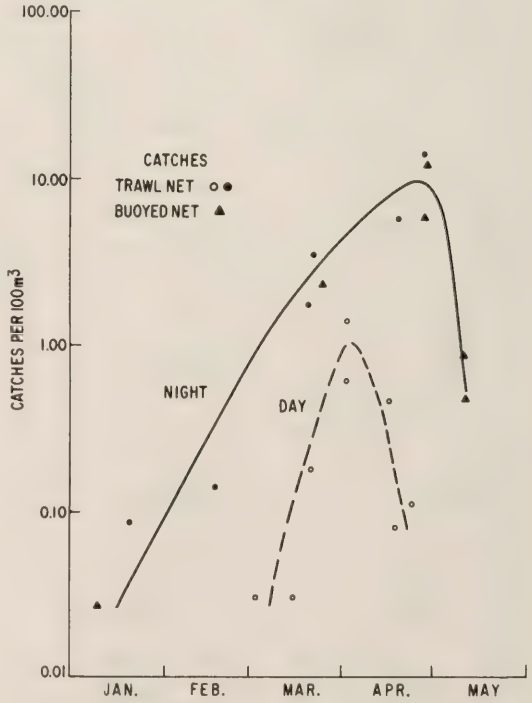

FIGURE 11.—Monthly progression of larval catches (larvae 36 mm and larger) in the Boothbay area from trawl tows at night and during the day and in the upper Sheepscot estuary from buoyed and anchored nets at night.

larvae appeared to grow about 1 mm every 5 days. Similarly, in 1964 modal lengths may be traced from late September to early November with an apparent larval growth of 1.3 mm every 5 days, but then the mode became difficult to identify.

DISCUSSION

SEASONAL CHANGES IN ABUNDANCE AND LARVAL LENGTH CAUSED BY MORTALITY

After larvae hatched and accumulated in the coastal bays and estuaries, their abundance was determined by the rate at which they died. The autumn mortality was especially severe, for the catch declined in the Boothbay area (Figure 6) despite the addition of successive broods to the area throughout the autumn. This high mortality was also indicated by the failure of length modes to persist into the winter. The number of larvae in a given mode apparently was reduced with time and coincidently with differential growth until the larvae were too sparse in the catches to form a distinguishable mode. In 1966 the disappearance of a mode of relatively large fish from the catch caused a sharp drop in the mean larval length during November (Figure 7). Although the mean length increased either with subsequent growth of the remaining larvae or with the addition of larvae to the area, it remained below the mean lengths of the other years throughout the winter. Winter mortalities were not as high as those in the autumn. Graham and Davis (1971) determined mortalities from December to January for larvae captured in the Sheepscot estuary during 1964-67 and recently for mortalities for 1968-69. Estimates for the 6 years varied from 22% to 52% for 15-day intervals and appeared statistically reliable with the largest spread in the 0.95 fiducial interval in 1968 (27.7-36.9%), and the smallest in 1966 (22.0-22.8%).

Extensive reductions in our catch rates in the late spring occurred from avoidance of the gear by the larvae and their departure from our sampling stations. Catches at the upper estuarine stations in the Boothbay area were larger than those at the lower and outer stations. Progressive peaks in abundance, that were present in the autumn, were absent from outer to upper estuarine stations in the spring. One explanation for the lack of progression is that the larger larvae moved landward so rapidly as to be undetected in the spring. Another and more likely explanation is that their mortality was sufficiently low to permit an accumulation of larvae at the landward extremity of their movement where numbers always greatly exceeded the number of larvae moving into the area.

Estimates of annual mortality were based on winter mortality (Graham and Davis, 1971) because measurements of total mortality during a given year were impracticable as they were influenced by larval movement in the autumn and in the spring. For most year classes, a higher winter mortality recorded in the upper end of the Sheepscot estuary coincided with a smaller maximum catch there in the subsequent spring. Also, higher winter mortalities usually coincided with a poorer condition or well-being of the larvae (Chenoweth, 1970) for the Boothbay area (Figure 12).

The causes of larval mortality along the western coast of the Gulf of Maine were not determined, but inferences were made by Chenoweth (1970) and by Sherman and Honey (1971). Essentially, they suggested that winter mortality might be related to lower lethal temperatures, inhibition of feeding by low temperatures, and a scarcity of food. Sherman (personal communication) found in recent studies that the larval guts were frequently occluded by parasites, which may cause death.

SEASONAL CHANGES IN DISTRIBUTION RELATED TO LARVAL SOURCES

After hatching, the larvae shifted their distribution from spawning areas to the coastal bays and estuaries. These destinations were apparent from our catches, but not all the sources or spawning areas were determined. The sources of larval herring in the Gulf of Maine, including the western coast, their movements from these

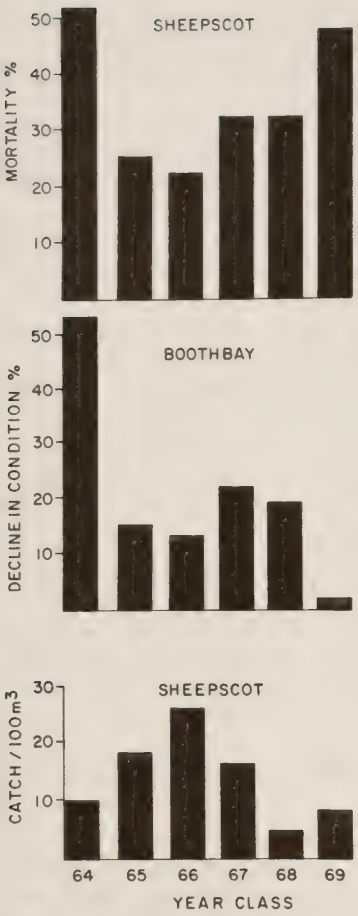

FIGURE 12.—A comparison among year classes of winter mortality of larvae in the Sheepscot estuary (upper panel), the decline in condition of larvae in the Boothbay area (center panel), and the subsequent spring catch rates in the Sheepscot (lower panel).

sources, and the resulting changes in their distributions have received attention from other investigators.

Spawning grounds of herring were located in the past by surveying the distribution of recently hatched larvae (Tibbo et al., 1958), and more recently by collecting eggs off the spawning grounds (Noskov and Zinkevich, 1967). Migrations of larvae from these grounds were traced by assuming that they were transported similarly to a particle of water. Thus, their paths of migration from the grounds were located within the residual currents at the surface. Boyar et al. (1971) reviewed such evidence for the Georges Bank-Gulf of Maine area and decided that larvae may enter the eastern sector of our sampling area from the spawning grounds off southwestern Nova Scotia, and that some larvae from Nova Scotia may be carried along the coast of Maine as far as Cape Cod, Mass. In a concurrent paper, Iles (1971) reported on the dispersion of larvae from southwest Nova Scotia and concluded from his data that the larvae were transported into the Bay of Fundy where they were retained during the winter. Boyar et al. (1971) also suggested that larvae entered the western sector of our coast from Jeffreys Ledge, Cashes Ledge, Stellwagen Bank, and other areas collectively just offshore of the coastal sector.

The larvae from these two sources, Nova Scotia and the ledges and banks in the southwestern Gulf of Maine, possibly contributed to the coastal larval population in the spring. Such a contribution would partially explain the high catch rates obtained in the Boothbay area where larvae accumulated in the autumn and spring. The autumnal movements of larvae into the area subsided by early December. The catch in the area at that time was less than the peak catch obtained in the subsequent spring, indicating that larvae present in autumn could not account for all of the larvae found in the same area in the spring. Much of the spring catch, therefore, may be formed by emigrants. Das (1968, see footnote 2) also discovered a similar emigration by examining length-frequency distributions of larvae in the coastal area of southwest Nova Scotia. And Sameoto (1971)[3] reached a similar conclusion from catches of larval herring entering St. Margaret Bay on the southeastern coast of Nova Scotia.

Another explanation for the differences in the early winter and the spring catches in our sam-

[3] Sameoto, D. D. 1971. The distribution of herring (*Clupea harengus L.*) larvae along the southern coast of Nova Scotia with some observations on the ecology of herring larvae and the biomass of macrozooplankton on the Scotian Shelf. Fish. Res. Board Can., Tech. Rep. 252, 72 p.

pling areas may be deduced from the residual surface currents. In winter, the direction of these currents is usually offshore; in spring, the currents are often directed inshore. Thus, larvae swept offshore in the winter might be returned to the coast in the spring. However, we did not detect any concerted movement by the larvae offshore in the winter and suspect that the assumption that larvae are transported similarly to a particle of water is often an oversimplification. The factors controlling the movement and retention of the larvae in shoal water must be investigated to understand the possibilities of their transport.

ANNUAL CHANGES IN ABUNDANCE AND THE FISHERY

The goal of this research was to choose an estimate of larval abundance or its correlate that could be used to predict the annual recruitment of immature 2-year-old herring to the sardine fishery of the western coast of the Gulf of Maine. Three different types of estimates were chosen: (1) winter mortality, (2) condition in the winter, and (3) maximum abundance in the spring. Sampling should continue over a number of years to determine whether the relations between the three measures have substance and whether any one or all of them are pertinent to predicting the abundance of 2-year-old herring.

A tentative comparison between the percentage of 2-year-old fish taken in the fishery with the percentage of winter mortality of the corresponding year class during 1964-68 is shown in Figure 13. Years of low mortality were usually related to subsequent greater percentage of 2-year-old fish in the fishery.

Estimates of winter condition are important because they provide an insight as to the cause of larval mortality. Because winter condition correlates with winter mortality, larval deaths are probably caused by debilitating factors such as disease, starvation, or parasitism. But, lack of agreement during 1969 (Figure 12) would involve other factors as well, such as predation or sudden and transient effects of man's activities within the coastal environment.

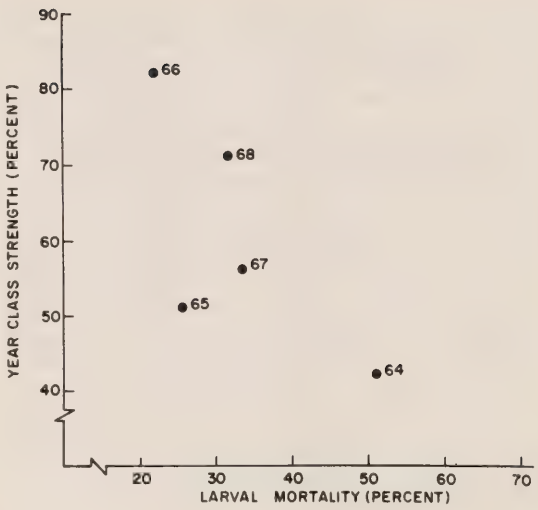

FIGURE 13.—Comparison between the percentage of 2-year-old herring captured in the Maine sardine fishery and the winter larval mortality for a given year class. Age composition of the fishery was determined by John E. Watson (personal communication). The catch also includes fish from the adjacent Canadian coast.

Estimates of abundance in the spring are necessary as well as winter mortality estimates because the number of larvae surviving until spring theoretically depends upon the initial number of larvae present by the end of autumn. During each of the years in which winter mortality was estimated in this study, the autumnal abundance was reduced to approximately the same level by early winter. During years of very successful hatching, the autumn mortality might not be sufficient to reduce the number of larvae to a level common to that of previous years. The subsequent spring abundance would then be determined by the initial number of larvae present in early winter as well as the winter mortality. The estimates of spring abundance in the Boothbay area and in the coastal area between Cape Small and Penobscot Bay (Figure 14) did not agree with the estimates obtained with buoyed and anchored nets in the Sheepscot for year classes 1964-65 (Figure 12, bottom panel). We do not understand the reason for this difference.

To date, monitoring of the winter mortality

and condition and spring abundance of larvae has been largely confined to the Boothbay area; the possibility of extending monitoring to other areas of the coast is being investigated. Nevertheless, events in the ecology of the larvae in the Boothbay area could represent those of the entire coast of the Gulf. Seasonal changes in larval abundance are similar along the coast and are comparable to those in the coastal area off southwest Nova Scotia (Das, 1968, see footnote 2) and on Georges Bank (Boyar et al., 1971). Yearly changes in oceanic conditions along the coast and in the offshore Gulf of Maine are also related (Colton, 1968). Further correlation between ecological events in the Boothbay area and those in other areas of the Gulf, at least adjacent areas, is evidenced by the agreement of the winter mortality estimates obtained in the Sheepscot and the subsequent spring abundance there. Larvae captured in the spring include emigrants from areas other than Boothbay. Correct forecasts of a poor fishery, to date, coincided with poor recruitment to the fishery; unfortunately, forecasts have not been made during years of good recruitment in the western sector.

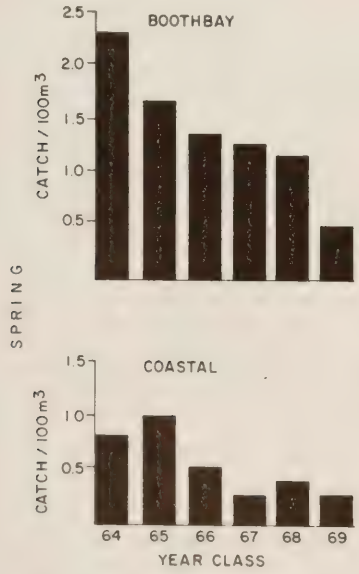

FIGURE 14.—Peak catches for larval herring in the spring among year classes 1964-69; in the coastal area between Cape Small and Penobscot Bay and in the Boothbay area.

SUMMARY OF ABUNDANCE AND DISTRIBUTION

The abundance and distribution of larval herring along the western coast of the Gulf of Maine is determined by their movements and mortality. Two inshore movements, one in the autumn and the second in the spring, are separated by a period of larval dispersal. Larvae hatch along the coast in autumn and penetrate the bays and estuaries. Their inshore movement decreases by early winter and in midwinter they disperse; at this time concentrations of larvae are infrequent inshore and along the coast. A second shoreward movement begins with the advent of spring. Larvae which hatched the previous autumn along the coast, and probably some which hatched beyond our sampling area, aggregate when making this shoreward movement. The inshore movement is completed by the end of spring when the majority of the larvae have assumed their adult form.

Mortality during the inshore movement in the autumn is very high. Although it is lower in the winter, mortality during this season may determine the abundance of larvae in the spring because the numbers are reduced by early winter to a relatively common level each year. The lower winter mortality may be related to the dispersal of the often weakened larvae; dispersal would reduce intraspecific competition for food and space. The lowest mortality occurs in the spring when the larvae are in good condition as shown by their ability to avoid high-speed trawls with large mouth openings.

The movement of the larvae shoreward within the complex currents of the coast is a striking feature of their coastal ecology.

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AN ECOLOGICAL STUDY OF GEORGIA COASTAL FISHES

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ABSTRACT

The distribution of fishes in relation to ecological factors was studied in a Georgia estuary and adjoining beach and coastal plain creek waters to establish fundamental base lines for the ecology of a relatively undisturbed section of the coast. The distributions of 168 fish species were related to nine recognizable habitats, temperature, and salinity. Length frequencies and spawning seasons were determined for most of the trawled species that contributed significantly to fish production in the estuary.

Collecting by a variety of techniques permitted evaluations of types of life cycles, of diversity in the various aquatic habitats, and of distribution patterns within the estuarine complex and adjoining waters. Numbers of species collected in nine aquatic habitats were as follows: beach - 114, lower reach of the estuary - 100, high marsh - 56, upper and middle reaches - 61, oligohaline creek - 40, fresh water - 39, tidal canal - 22, low-salinity tidal pool - 22, high-salinity tidal pool - 37.

Estuaries are highly productive and support important sport and commercial fisheries. A majority of the nation's commercial finfish and shellfish species and many coastal sport fishes utilize the estuarine environment during at least part of their life cycle. Estuaries are important recreational areas, especially for fishing, partly because of their proximity to civilization. Unfortunately, this proximity and lack of pollution controls have resulted in mass degradation of the nation's estuaries through pollution, filling, and dredging. Pre-pollution studies are essential for the precise evaluation of the ecological impact of stresses on estuaries. The normal functioning of estuaries must be understood before scientists can evaluate the effects of various stresses on estuaries. There is an urgent need to determine the significance of coastal habitats to the various life history stages of coastal fishes. The central Georgia coast presents an opportunity to study the ecology of fishes in a relatively undisturbed estuary and establish fundamental base lines for the detection and evaluation of pollution. Aspects of fish ecology that have been selected for examination include (1) distribution of fishes in relation to recognizable habitats, salinity, and temperature, (2) size frequencies and spawning seasons of many abundant species, (3) diversity of fishes in each of nine habitats, and (4) types of life cycles.

Except for the Brunswick and Savannah regions, Georgia estuaries are relatively free of pollution. However, certain Golden Isles along the Georgia coast are being considered for strip mining for titanium and phosphate. A nuclear power plant is under construction on the lower Altamaha River. Recent developments in the estuary studied herein include a kraft paper mill, a shrimp culture farm that may not be completed, and an interstate highway that may alter tidal flushing.

A complete picture of species distributions and size in coastal waters can be obtained only if all major habitat types are examined (Springer and Woodburn, 1960). Extensive trawling and seining were undertaken to achieve this goal. Comparisons with other studies are complicated by the difference in types and numbers of habitats sampled and differences in collecting methods.

There has been little work on the ecology of fishes of the U.S. Atlantic coast between Cape Hatteras, N.C., and northern Florida. Tagatz (1968) surveyed the fishes of St. Johns River,

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Fla. Tagatz and Dudley (1961) studied the seasonality of fishes in four coastal habitats near Beaufort, N.C. In South Carolina, Bearden (1961) published a field guide to the common marine fishes, compiled an unpublished list (1961) of marine fishes, and surveyed the elasmobranchs (Bearden, 1965). Lunz and Schwartz (1970) published an 18-year study of South Carolina coastal fishes.

Anderson (1968) surveyed the fishes caught by shrimp trawling from South Carolina to northeastern Florida from 1931 to 1935. His data are not tabulated here because many species complexes were identified only to genus and his collections were from regions other than the estuary under study. Miller and Jorgenson (1969) studied the seasonal abundance and length frequencies of fishes collected by seining at a beach habitat on St. Simons Island and at two high marsh stations, one near Jekyll Island and one near Meridian, Ga. They also listed the fishes collected at a freshwater station in the Altamaha River. Dahlberg and Heard (1969) surveyed the common elasmobranchs of the Georgia coast. Dahlberg and Odum (1970) demonstrated the trawl diversity of Georgia estuarine fishes collected over 14 months. Dahlberg (1971a)[2] presented an annotated list of the Georgia estuarine and coastal fishes. A section of an unpublished ecological survey (Dahlberg, 1971b)[3] was the basis for this report.

LOCATION AND DESCRIPTIONS OF HABITATS

Composition and diversity of fish species in nine aquatic habitats along the Georgia coast are compared in this study. Salinity, temperature, and some aquatic plants and animals that are characteristic of these habitats are given in Table 1.

[2] Dahlberg, M. D. 1971a. An annotated list of Georgia coastal fishes. *In* An ecological survey of the coastal region of Georgia, p. 255-300. Unpublished report to National Park Service from University of Georgia Institute of Natural Resources, Athens.

[3] Dahlberg, M. D. 1971b. Habitat and diversity of the fishes in North and South Newport Rivers and adjacent waters. *In* An ecological survey of the North and South Newport Rivers and adjacent waters with respect to possible effects of treated kraft mill effluent, p. 36-121. Unpublished report to Georgia Water Quality Control Board from University of Georgia Marine Institute, Sapelo Island.

TABLE 1.—Salinity, temperature, characteristic plants and animals of habitats studied, exclusive of freshwater creek habitat.

Sapelo Island Beach

Salinity—Range was 25.0 to 31.3‰ except when flood waters reduced salinity. Measured at 6.8 to 7.7‰ along south end of beach and 15.2‰ in surf near Big Hole at low tide in April 1970.

Plants—Sea oats *(Uniola paniculata)* are the most conspicuous plant on dunes along the beach.

Invertebrates seined or observed—Ghost crab *(Ocypode quadrata)*, polychaete worm tubes *(Onuphis microcephala,* and *Diopatra cuprea)*, horseshoe crab *(Limulus polyphemus)*, hermit crabs *(Clibanarius vittatus,* and *Pagurus longicarpus)*, gastropods *(Busycon carica,* and *Nassarius)*, sea cucumber *(Thyone briareus)*, sand dollar *(Mellita quinquiesperforata)*, isopod *(Aegothoa oculata)*, white shrimp *(Penaeus setiferus)*, shrimp *(Palaemonetes pugio)*, blue crab *(Callinectes sapidus)*, and squid *(Lolliguncula brevis)*.

Lower Reach of the Estuary - Trawl Stations 1-9, 12-14

Salinity—Averages for these stations ranged from 21.4 to 28.9 ‰ from 1967 to 1970 (Dahlberg et al., 1971, see text footnote 3).

Temperature—Averages for the 12 stations ranged from 8.1° (January) to 31.2°C (August).

Plants—Cord grass *(Spartina alterniflora)* is the dominant plant.

Invertebrates—Commercial species are white shrimp, brown shrimp *(Penaeus aztecus)*, and pink shrimp *(P. duorarum)*, American oyster *(Crassostrea virginica)*, and blue crab. Other common species are too numerous to list here.

High Marsh

Salinity—Generally 15 to 30‰.

Plants—*Spartina alterniflora* and *Juncus roemerianus* are characteristic.

Middle and Upper Reaches

Salinity—Range was 11.7 to 29.0‰ and average was 21.2‰ at lowermost station, trawl station 10. Range was 0.3 to 18.7‰ and average was 5.3‰ at uppermost station (F).

Temperature—Range was 8.3° to 31.7°C and average was 20.9°C at the lowermost station, trawl station 10. Range was 9.0° to 30.0°C and average was 21.5°C at uppermost station, station F.

Aquatic plants—*Spartina alterniflora, Juncus roemerianus,* tall cord grass *(Spartina cynosuroides)*, marsh elder *(Iva frutescens)*, bulrush *(Scirpus robustus)*, primrose-willow *(Jussiaea)*.

TABLE 1.—Continued.

Sapelo Island Beach—Cont.

Semiaquatic invertebrates—*Uca pugnax, Sesarma, U. pugilator.*
Aquatic invertebrates that were seined, in decreasing order of abundance—*Palaemonetes pugio*, white shrimp, blue crab, *Palaemonetes vulgaris*, brown shrimp.

Riceboro Creek in vicinity of U.S. Highway 17 (oligohaline)

Salinity—Range was 0 to 13.6‰ and average was 3.0‰ for 1968-70.
Temperature—Range was 3.5° to 30.5°C and average was 21.2°C for 1968-70.
Aquatic plants—*Spartina alterniflora, Juncus roemerianus*, waterwort *(Elatine americana)*, spike-rush *(Eleocharis acicularia)*, *Iva frutescens, Spartina cynosuroides*, saw grass *(Cladium jamaicense)*, groundsel-tree *(Baccharus halimifolia)*, arrowhead *(Sagittaria)*, water hemlock *(Cicuta maculata)*, *Jussiaea* sp., *Scirpus robustus, Scirpus* sp., salt grass *(Distichlis spicata)*, mock bishop-weed *(Ptilimnium capillaceum)*, sedge *(Cyperus virens)*, and beak rush *(Rhynchospora* sp.).
Invertebrates of lower Riceboro Creek, in decreasing order of abundance in net collections—*Palaemonetes pugio*, blue crab, white shrimp, *Rhithropanopeus harrisi*, and brown shrimp. Other invertebrates of lower Riceboro Creek, reported in Heard and Heard (1971)[1] and Heard and Sikora (In press) include crabs *(Uca minax*, and *Sesarma cinereum)*, amphipods *(Corophium* sp., *Orchestia grillus, O. uhleri, Gammarus tigrinus, Corophium lacustre*, and *Melita nitida)*, isopods *(Cyathura polita, Cassidinidea lunifrons, Munna reynoldsi, Sphaeroma destructor*, and *Ligia exotica)*, tanaid *(Leptochelia)*, barnacle *(Balanus improvisus)*, polychaetes *(Namalycastis abiuma*, and *Nereis succinea)*, gastropods *(Littoridinops tenuipes, Hydrobia, Detracia floridana*, and *Melampus bidentatus)*, clams *(Cyrenoidea floridana*, and *Polymesoda carolinae).*

Tidal canal

Salinity—Range was 0.3 to 23.2‰.
Temperature—Range was 8.0° in February 1968 to 30.1°C in August 1967.
Aquatic plants—*Iva frutescens, Borrichia frutescens, Spartina alterniflora, Juncus roemerianus*, glasswort *(Salicornia virginica)*, and *Distichlis spicata.*
Semiaquatic invertebrates—*Uca minax, U. pugilator*, and *Sesarma* sp.
Aquatic invertebrates seined, listed in decreasing order of abundance—*Palaemonetes pugio*, white shrimp, blue crab, and brown shrimp.

Low-salinity tidal pools

Salinity—Range was 0 to 24.4‰.
Temperature—Range was 7.3° (January 1970) to 28.2°C (September 1969).
Marsh plants—*Spartina alterniflora, Juncus roemerianus, Salicornia virginica, Eleocharis* sp., *Bacopa monnieri*, aster *(Aster tenuifolius), Distichlis spicata, Scirpus* sp., and *Iva frutescens.*
Semiaquatic invertebrates—*Uca minax, U. pugilator*, and *Sesarma* sp.
Aquatic invertebrates—*Palaemonetes pugio*, and blue crab (juvenile).

High-salinity tidal pools

Salinity—Range was 14.7 to 34‰ in "east pools" and 13.1 to 30.3‰ in "west pools."
Temperature—Range was 8°C in January and February to 32°C in July, August, and September.
Marsh plants along road bank—*Iva frutescens, Borrichia frutescens, Baccharus halimifolia, B. angustifolia* - false willow.
Marsh plants occurring below road bank in the marsh—*Spartina alterniflora, Juncus roemerianus, Salicornia virginica, Distichlis spicata, Batis maritima*, and *Aster tenuifolius.*
Semiaquatic invertebrates—*Sesarma* sp., *Uca pugnax, U. pugilator*, and *U. minax* (uncommon).
Aquatic invertebrates seined, listed in decreasing order of abundance—*Palaemonetes pugio*, blue crab, white shrimp, and brown shrimp.

[1] Heard, R. W., Jr., and E. J. Heard. 1971. Notes on the natural history and invertebrate fauna of the Upper North Newport River. *In* An ecological survey of the North and South Newport Rivers and adjacent waters with respect to possible effects of treated kraft mill effluent, p. 234-246. Unpublished report to Georgia Water Quality Control Board from University of Georgia Marine Institute, Sapelo Island.

Figure 1 illustrates the estuarine complex that was studied, with the exception of the freshwater and Sapelo Island stations. Figure 2 gives locations of stations in the upper part of the North Newport River and oligohaline region in relation to the paper mill (station G), creeks, marsh, railroad, highway, and proposed expressway.

An estuary ranges from the oligohaline creeks to the sounds and barrier islands. Ocean beaches are generally not considered as part of the estuary even though the outflow from estuaries, at least in Georgia, affects beaches and offshore areas where the highly turbid and productive estuarine waters are visible to several miles offshore. This study attempts to evaluate the ecological importance of the following seven estuarine habitats and adjoining beach and freshwater habitats to coastal fish populations. The habitat divisions are somewhat arbitrary as they are all interrelated parts of a single aquatic ecosystem along the coast.

Habitat 1: Sapelo Island Beach (Figure 3).—This station is the ocean beach on Sapelo Island and is known locally as Nannygoat Beach. This beach extends between Dean Creek at the south end and a lagoon (Big Hole) that separates the north end of this beach from Cabretta Island. Most samples were taken in the surf zone near

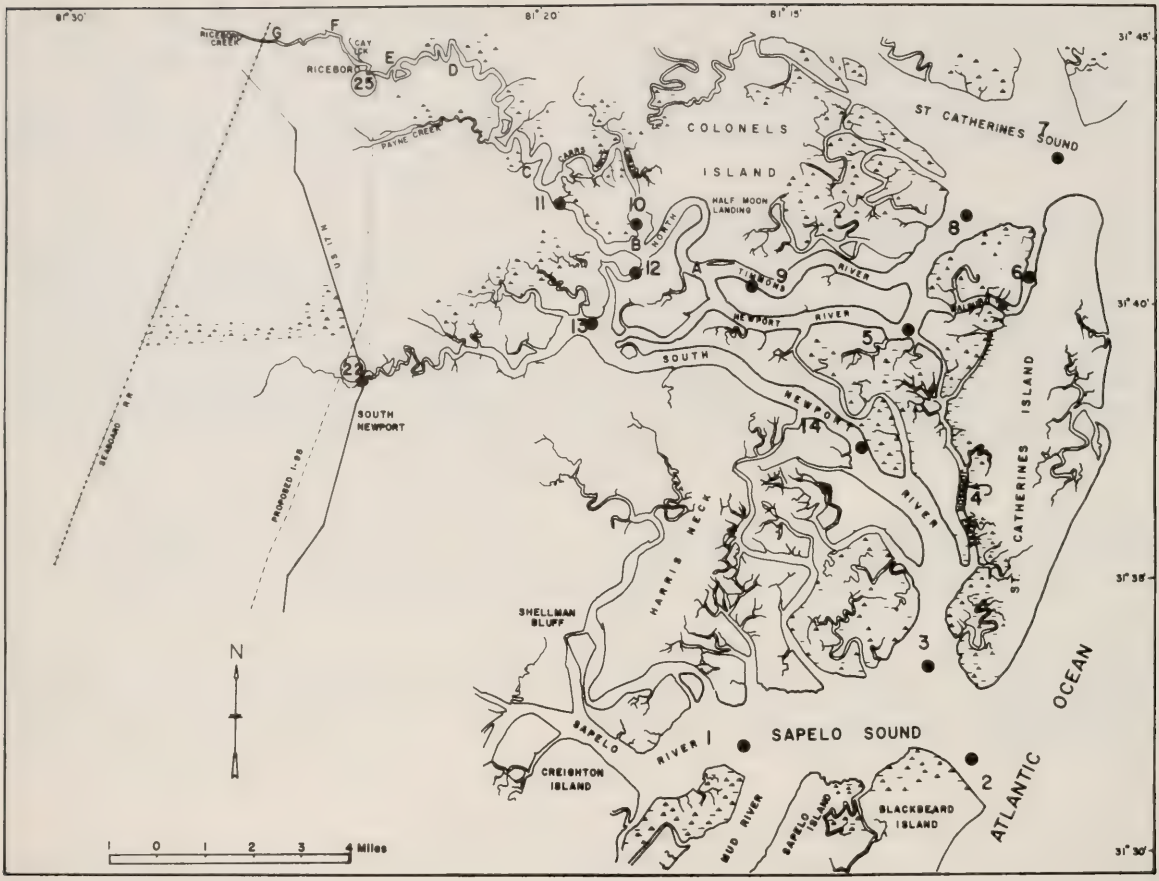

FIGURE 1.—Study area and sampling stations on Georgia Coast except for Sapelo Island and freshwater stations. Numbers 1-14 are trawl stations and associated dots are approximate centers of drags. Letters A-G are stations that were reached with a small boat. Circled numbers are mile points.

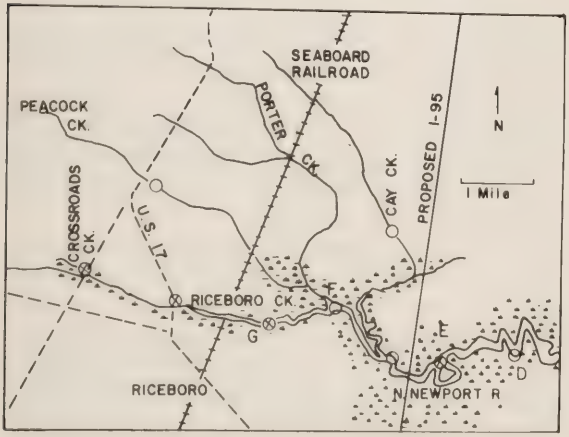

FIGURE 2.—Oligohaline creeks and upper reach of the estuary. Circles are stations sampled for physico-chemical data and circles with an X are fish sampling stations. The Interstate Paper Corp. outfall is at station G. Dashed lines represent highways.

the junction of the road and the beach. Because collecting was generally unproductive in the surf zone at high tide, this station was occupied near low tide. Furthermore, concentrations of fishes in the intertidal sloughs were isolated from the ocean only at low tide.

The continuity of the south end of Sapelo Beach and the lower reach (Doboy Sound) make

FIGURE 3.—View of Sapelo Beach at low tide with Atlantic Ocean and shrimp boat in background and an intertidal slough in center. Fishes become concentrated and trapped in these sloughs at low tide.

it necessary to arbitrarily define the beach habitat to include waters occurring within the wading depth of collectors (about 4 ft). The station is subject to tidal changes—tide ranges from 4.5 to 10.5 ft and has a mean of 6.8 at Sapelo Island (Ragotzkie and Bryson, 1955).

Habitat 2: Lower reach of the estuary. — This habitat includes the sounds and polyhaline river stations. My records for this habitat are based primarily on trawl collections at stations 1-9 and 12-14 (Figure 1). A temperature-salinity diagram (Figure 4) does not indicate any relation between these factors.

Habitat 3: High marsh. — This habitat is the upper section of the littoral zone in the salt marsh. I sampled pools behind high marshes and a tidal ditch in a high marsh but not the high marsh proper. Fishes of this habitat were thoroughly surveyed by Miller and Jorgenson (1969) and are listed in column three of Table 2. Their marsh stations were located near Jekyll Island and near Doboy Sound. The substrate of this habitat is sand and mud that is firm enough to walk on, as opposed to the low marsh which has a soft mud substrate.

Habitat 4: Middle and upper reaches of the estuary (Figures 2 and 5). — The middle reach

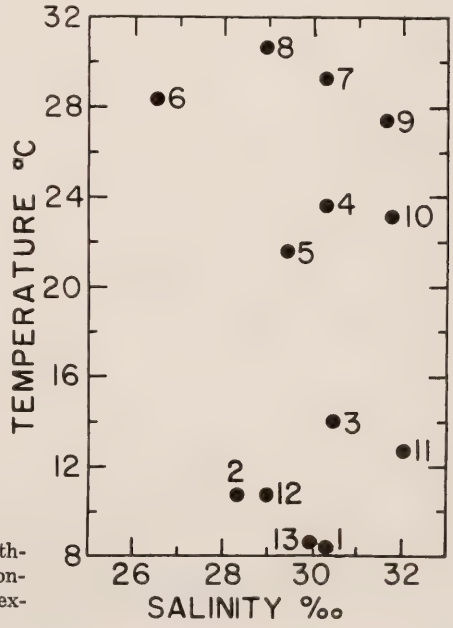

FIGURE 4.—Temperature-salinity diagram for St. Catherines Sound at trawl station 7. Numbers represent consecutive months from January 1968 to January 1969 except 12 is December 1969.

TABLE 2.—Distribution of fishes among the study habitats—1, beach; 2, lower reach; 3, high marsh; 4, middle and upper reaches; 5, oligohaline creek; 6, freshwater creek; 7, tidal canal; 8, low-salinity tidal pool; and 9, high-salinity tidal pool. Names are in phylogenetic order, following Bailey (1970). Parentheses indicate records not taken at regular stations. Boldface indicate record is based on one collection by either the author or Miller and Jorgenson (1969). Asterisk indicates that young of the species are common in the estuary or beach waters. All high marsh records are from Miller and Jorgenson (1969).

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Orectolobidae									
Ginglymostoma cirratum	(X)	(X)							
Carcharhinidae									
**Aprionodon isodon*	(X)	(X)							
Carcharhinus acronotus	(X)	(X)							
**Carcharhinus limbatus*	(X)	X							
**Carcharhinus milberti*	(X)	(X)							
Galeocerdo cuvieri	(X)	(X)							
**Negaprion brevirostris*	X	(X)							
Sphyrnidae									
**Sphyrna lewini*	(X)	(X)							
Sphyrna tiburo		X							
Squalidae									
Squalus acanthias		X							
Rhinobatidae									
Rhinobatis lentiginosus		X							
Rajidae									
Raja eglanteria		X							
Dasytidae									
**Dasyatis americana*	(X)	X							
**Dasyatis sabina*	X	X		X					
Dasyatis sayi	(X)	X							
**Gymnura micrura*		X		X					
Myliobatidae									
Rhinoptera bonasus	(X)	(X)							
Lepisosteidae									
Lepisosteus osseus		X		X	X	X			
Lepisosteus platyrhincus						X			
Elopidae									
**Elops saurus*	X		X	X			X	X	X
**Megalops atlantica*	(X)	X					X	X	X
Albulidae									
Albula vulpes	(X)								
Anguillidae									
**Anguilla rostrata*			X		X	X		X	X
Ophichthidae									
Myrophis punctatus	(X)		X		X				
Ophichthus gomesi		X							
Clupidae									
Alosa aestivalis		(X)	X	(X)	(X)	(X)			
Alosa mediocris	(X)	X		(X)	(X)	(X)			
**Alosa sapidissima*		X		X	(X)	(X)			
Brevoortia smithi	X		X				X		X
**Brevoortia tyrannus*	X	X	X	X	X		X	X	X
Dorosoma cepedianum	(X)	(X)	X	X	X	(X)			
**Dorosoma petenense*	X		X				X		
Harengula pensacolae	X	X	X						
**Opisthonema oglinum*	(X)	X	X						
Sardinella anchovia	(X)								

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Engraulidae									
Anchoa cubana	(X)								
**Anchoa hepsetus*	X	X	X	X					
Anchoa lyolepis	(X)								
**Anchoa mitchilli*	X	X	X	X	X				X
Esocidae									
Esox americanus					X	X			
Umbridae									
Umbra pygmaea						X			
Synodontidae									
Synodus foetens	(X)	X			X				
Cyprinidae									
Notemigonus crysoleucas					X	X			
Notropis maculatus						X			
Catostomidae									
Erimyzon sucetta						X			
Ictaluridae									
**Ictalurus catus*				X	X	X			
Ictalurus natalis						X			
Noturus gyrinus					X	(X)			
Ariidae									
**Bagre marinus*	(X)	X		X					
**Arius felis*	X	X		X					
Amblyopsidae									
Chologaster cornuta						X			
Aphredoderidae									
Aphredoderus sayanus					X	X			
Batrachoididae									
**Opsanus tau*	X	X		X					
Gobiesocidae									
**Gobiesox strumosus*		X		X					
Antennariidae									
Antennarius radiosus	(X)								
Histrio histrio	(X)								
Gadidae									
**Urophycis floridanus*		X		X					
**Urophycis regius*	(X)	X		X					
Ophidiidae									
Rissola marginata	(X)	X		X					
Belonidae									
Strongylura marina	X	X	X	X					
Cyprinodontidae									
**Cyprinodon variegatus*	X		X				X	X	X
Fundulus chrysotus						X			
**Fundulus confluentus*					X	X		X	
**Fundulus heteroclitus*	X	X	X	X	X		X	X	X
**Fundulus luciae*	(X)		X						
**Fundulus majalis*	X		X				X		X
Fundulus notti						X			

TABLE 2.—Continued.

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Cyprinodontidae—Cont.									
Leptolucania ommata						X			
Lucania goodei						X			
Poeciliidae									
**Gambusia affinis*	X		X		X	X	X	X	X
Heterandria formosa			X		X	X			
**Poecilia latipinna*	(X)		X		X		X	X	X
Atherinidae									
**Membras martinica*	X	X	X						
**Menidia beryllina*	X			X	X	X			
**Menidia menidia*	X	X	X	X					X
Syngnathidae									
Hippocampus erectus		X							
**Syngnathus fuscus*	X	X		X	X				
**Syngnathus louisianae*	X	X	X	X	X				X
Centropomidae									
**Centropomus undecimalis*							X	X	X
Serranidae									
Centropristis philadelphica	(X)	X							
Centropristis striata		X		X					
Centrarchidae									
Acantharchus pomotis						X			
Centrarchus macropterus					X	X			
Elassoma evergladei						X			
Elassoma zonatum						X			
Enneacanthus gloriosus						X			
Enneacanthus obesus						X			
Lepomis auritus					X	X			
Lepomis gulosus					X	X			
Lepomis macrochirus					X	X			
Lepomis marginatus						X			
Lepomis punctatus					X	X			
Micropterus salmoides					X	X			
Percidae									
Ethrostoma fusiforme						X			
Pomatomidae									
Pomatomus saltatrix	X	X	X	X					
Echeneidae									
Echeneis naucrates	(X)	(X)							
Carangidae									
Caranx hippos	X	(X)	X	X					X
Caranx latus	(X)								
**Chloroscombrus chrysurus*	X	X	X	X					X
**Oligoplites saurus*	X		X	X					X
Selene vomer	X	X							
**Trachinotus carolinus*	X		X						
**Trachinotus falcatus*	X		X						
Trachinotus goodei	(X)								
Vomer setapinnis	(X)								
Lutjanidae									
Lutjanus griseus	(X)	(X)	X					X	X

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Gerreidae									
**Diapterus olisthostomus*	X		X		X		X	X	X
**Eucinostomus argenteus*	X	X	X	X	X		X	X	X
Eucinostomus melanopterus					X				
Pomadasyidae									
Orthopristis chrysoptera	(X)	X		X					
Sparidae									
**Archosargus probatocephalus*	(X)	(X)	X						
**Lagodon rhomboides*	(X)	X	X				X	X	X
Sciaenidae									
**Bairdiella chrysura*	X	X	X	X	X		X	X	X
**Cynoscion nebulosus*	(X)	X	X	X					X
**Cynoscion nothus*		X							
**Cynoscion regalis*	X	X	X	X			X		X
**Larimus fasciatus*	X	X							
**Leiostomus xanthurus*	X	X	X	X	X		X	X	X
**Menticirrhus americanus*	X	X	X	X					
**Menticirrhus littoralis*	X	X	X						
**Menticirrhus saxatilis*	X	X	X						
**Micropogon undulatus*	X	X	X	X	X		X		X
**Pogonias cromis*	(X)	X	X				X	X	X
**Sciaenops ocellata*	X	(X)	X				X	X	X
**Stellifer lanceolatus*	X	X		X					
Kyphosidae									
Kyphosus incisor	(X)								
Ephippidae									
**Chaetodipterus faber*	X	X	X	X					
Pomacentridae									
Abudefduf saxatilis	(X)								
Mugilidae									
**Mugil cephalus*	X	(X)	X	X	X		X	X	X
**Mugil curema*	X	(X)	X	X			X	X	X
Sphyraenidae									
Sphyraena guachancho	X								
Sphyraena picudilla	(X)								
Uranoscopidae									
**Astroscopus y-graecum*	X	X	X	X					
Blenniidae									
**Chasmodes bosquianus*	(X)	(X)							
Hypleurochilus geminatus	(X)	X							
**Hypsoblennius hentzi*	(X)	X		X					
Eleotridae									
**Dormitator maculatus*								X	
Gobiidae									
Evorthodus lyricus									(X)
**Gobionellus boleosoma*	X		X						X
Gobionellus hastatus		X							X
**Gobionellus shufeldti*	(X)							X	
Gobionellus smaragdus									X
**Gobiosoma bosci*	X	X	X	X	X				
**Gobiosoma ginsburgi*	(X)	(X)							X
Microgobius thalassinus									X

TABLE 2.—Continued.

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Trichiuridae									
Trichiurus lepturus	(X)	X							
Scombridae									
Scomberomorus cavalla	(X)								
Scomberomorus maculatus	X	X							
Stromateidae									
Peprilus alepidotus	X	X		X					
Peprilus triacanthus	(X)	X		X					
Triglidae									
**Prionotus carolinus*	(X)	X							
**Prionotus evolans*	X	X	X	X					
Prionotus salmonicolor		X							
**Prionotus scitulus*	(X)	X		X					
**Prionotus tribulus*	(X)	X		X					
Bothidae									
**Ancylopsetta quadrocellata*		X		X					
Citharichthys spilopterus	(X)	X		X	X				

Family and species	Habitat								
	1	2	3	4	5	6	7	8	9
Bothidae—Cont.									
Etropus crossotus	(X)	X		X					
Paralichthys albigutta	(X)	X							
**Paralichthys dentatus*	X	X		X					
**Paralichthys lethostigma*	X	X	X	X	X				
Paralichthys squamilentus	X								
Scophthalmus aquosus	X	X		X					
Soleidae									
**Trinectes maculatus*	(X)	X		X	X	X			
Cynoglossidae									
**Symphurus plagiusa*	X	X	X	X	X				X
Balistidae									
Monacanthus hispidus	X	X	X	X					
Tetraodontidae									
Sphoeroides maculatus	X	X	X						
Diodontidae									
Chilomycterus schoepfi	X	X	X	X					

includes the North Newport River and lower parts of its tributaries from the lower end of Carrs Neck Creek (trawl station 10) upstream to station C. The upper reach extends from Payne Creek to the mouth of Riceboro Creek (station F). I generally treat these two sections as a unit for convenience.

Because salinity varies so greatly, this section of the estuary only roughly corresponds to the zones recognized by Carriker (1967). He recognized salinity ranges of 5 to 18‰ for the upper reach and 18 to 25‰ for the middle reach.

Habitat 5: Oligohaline creek (Figure 6). — The North Newport River originates at the confluence of Peacock and Riceboro Creeks. Oligohaline sampling stations were located in the oligohaline section of Riceboro Creek (Figure 2). Most fishes were collected in Riceboro Creek at station G and the lower part of Crossroads Creek where it joins Riceboro Creek near the town of Crossroads. Crossroads Creek was recently diverted into Riceboro Creek above the station by the State Highway Department, thus eliminating the station. Salinity and temperature ranges are given in Table 1. A temperature-salinity diagram (Figure 7) indicates that salinity generally increased with rising tide except when fresh water prevailed throughout the tidal cycle. In winter water temperatures were lowest at low tides.

Habitat 6: Freshwater creek. — Seven freshwater or limnetic stations in Coastal Plain creeks, free from the influence of salt water, are called "freshwater stations" in the text. The first six of these stations are in the North Newport River drainage in Liberty County and were sampled on 13 May 1968. The seventh is in the Ogeechee drainage in Chatham County and was occupied on 9 March 1969. Location of these collections are as follows: (1) Upper South Newport River at U.S. Highway 17; (2) Headwaters of Payne Creek on U.S. Highway 17, 2 miles west of Riceboro; (3) Tributary of Riceboro Creek about 2.5 miles north of Crossroads on a county road; (4) Peacock Creek, 2 miles southeast of McIntosh, on dirt road off U.S. Highway 82; (5) Goshen Swamp Creek on U.S. Highway 82, 2 miles south of Flemington; (6) Peacock Creek at Solomon Temple, between

FIGURE 5.—A muddy sand bar exposed at low tide at the mouth of Payne Creek where fishes were seined. *Spartina alterniflora* is visible on the right and the "back marsh" contains *S. alterniflora* and *Juncus roemerianus*. Hammocks and larger islands in this region are bordered by salt marshes and tidal creeks.

FIGURE 6.—Riceboro Creek near high tide at the Seaboard Railroad bridge. A variety of invertebrates are associated with the diverse intertidal flora, roots, and debris found in this oligohaline creek.

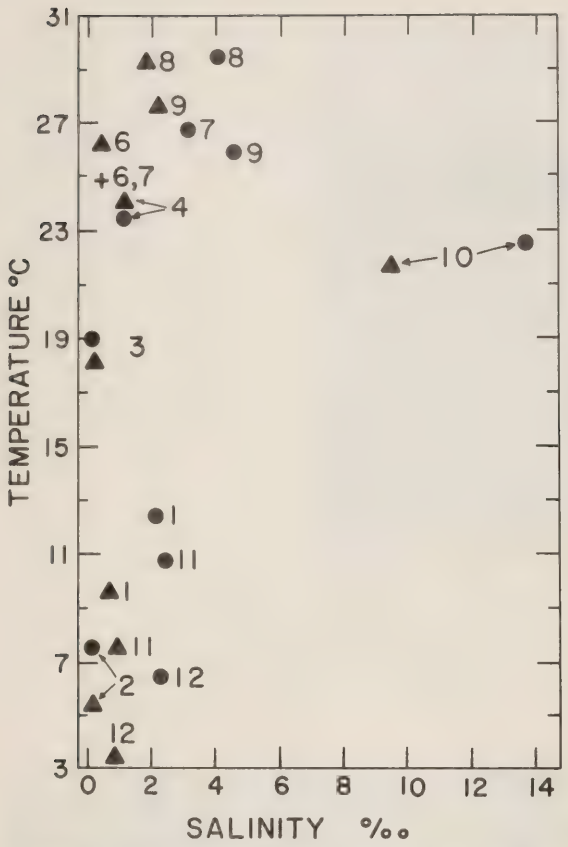

FIGURE 7.—Temperature-salinity diagram for Riceboro Creek at U.S. Highway 17; Numbers 1-4 are months of January through April 1969, and 6-12 are June through December 1968. Circles are high tide readings and triangles are low tide readings. Cross is high tide value for June and low tide value for July.

Midway and McIntosh on dirt road off U.S. Highway 82; (7) Tributary of Ogeechee River at U.S. Highway 17 near the Ogeechee River bridge.

Habitat 7: Tidal canal — This station is a runoff ditch or canal located in the marsh on the west side of Sapelo Island, 3.4 miles north of the Sapelo airport. This ditch is open to a polyhaline river (Mud River) at all tide levels and its mud banks are under several feet of water at high tide. Water depth was 3 to 4 ft at low tide in the deepest section, which was located at the end of a road culvert on the salt marsh side of a road.

Habitat 8: Low-salinity tidal pools — Two small pools located next to the road on the west side of Sapelo Island are treated together in the text. These pools are located 4.1 miles north of the Sapelo airport on the west side of the road. Runoff water flooding through a culvert opening into the lower and larger pools has eroded the bottom to a depth of approximately 5 ft. A higher culvert opening to the upper and smaller pool rarely has runoff water. This pool is 3 to 4 ft deep. At low tide only trickles of water connect the two pools and drain the lower pool through the marsh. Located behind the high marsh, these pools are flooded by Mud River only on high tide.

Habitat 9: High-salinity tidal pools (Figure 8). — These are a series of artificial pools located on the south end of Sapelo Island along a road leading to the Sapelo lighthouse, hence the local name lighthouse ponds. The pools are located behind a high marsh characterized by *Spartina alterniflora* and *Juncus roemerianus*. The pool sampled on the west side of the road is flooded by waters from South End Creek and the Marine Institute's boat basin. Two pools sampled on the east side of the road are connected at high tide and are flooded by waters from Deans Creek. *Palaemonetes pugio* was abundant in seine collection, except during the coldest weeks when the water temperature approached 8°C. At this time the fishes were also scarce or absent, and the relatively sterile and clear water allowed the author to see the bottom of the pools whereas the water was very turbid during other months.

METHODS

I seined shallow estuarine habitats (habitats 1, 5, 7, 8, and 9 and 4 in part) with a 35-ft (10.7-m) seine having ¼-inch (6.35-mm) bar mesh; a 10-ft (3.05-m) version was used in freshwater creeks. For habitat 3 I used the records of Miller and Jorgenson (1969) who collected with 40- and 70-ft (12.2- and 21.4-m) bag seines. Their records for St. Simons Island Beach are included in the list for habitat 1.

Habitat 2 (trawl stations 1-9, 12-14 in Figure 1) and the lower part of habitat 4 (trawl

FIGURE 8.—Tidal "borrow pool" on west side of road to lighthouse on Sapelo Island. Zonation of dominant plants along road bank generally from left to right in picture: wax myrtle (*Myrica cerifera*), groundsel-tree (*Baccharus halimifolia*), marsh elder (*Iva frutescens*), and sea ox-eye (*Borrichia frutescens*). *Juncus roemerianus* and *Spartina alterniflora* are dominant along the pool bank. There is an abundance of crabs (*Uca* spp. and *Sesarma* sp.) in both the harder and softer substrates between the pool and the road.

stations 10 and 11) were sampled on RV *Kit Jones* cruises, each station for 15 min with a 20-ft (6.1-m) otter trawl which had 1¼-inch (32-mm) stretched mesh in the bag. Each of the 14 trawl stations was sampled about 37 times from January 1967 through December 1969 except for stations 6, 8, 12, and 13, which were sampled 33 or 34 times and then discontinued. Five trawl samples were lost for various reasons including snags at station 9 on two occasions.

All Sapelo Island habitats (1, 7, 8, and 9) were sampled during all four seasons and about 20 times from April 1967 through February 1970.

Habitat 4 was sampled primarily with a 20-ft (6.1-m) trawl and a 35-ft (10.7-m) seine. The two trawl stations (10 and 11) are the uppermost of the 14 stations sampled with the RV *Kit Jones* from January 1967 through December 1969. Seining stations were sand bars that were exposed only near low tide. Regular stations were at the lower end of Carrs Neck Creek (mile point 10 = 16.1 km) and the mouth of Payne Creek (mile point 15.4 = 24.8 km). These stations were seined approximately monthly from June 1969 to May 1970. In addition 22 collections were made between the upper end of Carrs Neck Creek and mouth of Riceboro Creek with the seine, a cast net, and a 10-ft (3.05-m) trawl towed by an outboard motor boat.

In habitat 5 most fish collections were seined at low tide at a muddy sand bar (station G) between the Seaboard Railroad tracks and the effluent outfall of the Interstate Paper Corp. Trawling (10-ft trawl) was most fruitful in the winter. Seine and dip-net collections were made at the Crossroads station.

A few additional collections were made with a 100-ft (30.5-m) seine in habitat 1, by angling in habitats 1 and 2 (Dahlberg and Heard, 1969),

and by dip net in habitat 8 and in Riceboro Creek at the Seaboard Railroad.

All specimens were preserved in 10% formaldehyde solution and analyzed in the laboratory except when numbers in trawls were too large to retain more than a sample. Representatives of all species were retained at the Marine Institute.

The phylogenetic order and names recommended by Bailey (1970) are followed herein.

HABITATS OF COASTAL FISHES

ORDER SQUALIFORMES - SHARKS

Ten species of sharks (Table 2) were collected in this study and by Dahlberg and Heard (1969). Nearly all specimens, bonnethead excepted, were caught with fishing poles at the beach and in the sounds. Only three sharks were trawled, one each of the spiny dogfish (*Squalus acanthias*), bonnethead (*Sphyrna tiburo*), and the blacktip shark (*Carcharhinus limbatus*).

Most shark species have distinct seasonal migratory patterns. Carcharhinid sharks apparently migrate into the estuary during the warm months as all six were collected from June to September. The spiny dogfish is a cold-water species that migrates into Georgia estuaries during the coldest months (Dahlberg and Heard, 1969); it was collected only in January and February.

ORDER RAJIFORMES - SKATES AND RAYS

The Atlantic guitarfish (*Rhinobatos lentiginosus*) and clearnose skate (*Raja eglanteria*) are most common in the ocean and were not collected farther up the estuary than the sounds. Although the guitarfish was collected only in May and June, the skate was taken throughout the year.

Three stingrays of the genus *Dasyatis* (Table 2) are common in the sounds and shallow waters along the beaches. The Atlantic stingray (*D. sabina*) was the most abundant of the three species taken by trawling and angling. It was commonly trawled in the middle reach of the estuary at salinities as low as 9.9‰. This species is euryhaline (Gunter, 1956).

The smooth butterfly ray (*Gymnura micrura*) was collected by trawl in the estuary as far up as the middle reaches but not at salinities lower than 24.4‰.

ORDER SEMIONOTIFORMES

Lepisosteidae - gars

Two species of *Lepisosteus* were taken in the study area. The Florida gar (*L. platyrhincus*) occurred only at freshwater station 2. The euryhaline longnose gar (*L. osseus*) was abundant and was often seen or trawled in fresh and brackish waters throughout the year. The longnose gar has been collected in the ocean off Georgia.

ORDER ELOPIFORMES

Elopidae - tarpons

Small ladyfish (*Elops saurus*) were common in enclosed waters of tidal pools and the tidal ditch. Only two specimens were collected in open waters, one at Sapelo Beach and one in the upper reach of North Newport River. The ladyfish was common in both the high- and low-salinity pools at a salinity range of 0.1 to 28.7‰. It entered the pools in May and remained until November when the temperature was 19.9°C.

Small tarpon (*Megalops atlantica*) were common in enclosed waters of tidal pools and the tidal ditch, and large tarpon were often hooked by anglers along Sapelo Beach. Young were collected only from July to October at a temperature range of 20.0° to 31.9°C and were more common in the low-salinity pools than the high-salinity pools; the recorded salinity range was 0.1 to 24.8‰. Rickards (1968) found tarpon at Sapelo Island from July to November at salinities of 0.0 to 22.3‰ and temperatures of 16° to 36°C.

Albulidae - bonefishes

Inclusion of the bonefish (*Albula vulpes*) in Table 2 is based on a record from St. Simons Beach (Miller and Jorgenson, 1969).

ORDER ANGUILLIFORMES

Anguillidae - freshwater eels

The catadromous American eel (*Anguilla rostrata*) was widely distributed and abundant in the freshwater habitat and the high-salinity pools, but absent from trawl stations. All small specimens (54-170 mm) occurred in low salinities (0-1.9‰) in the freshwater and oligohaline creeks, and the low-salinity pools. Large specimens (230-470 mm) occurred primarily in saline waters (13.1-30.3‰) but one was collected in fresh water.

Ophichthidae - snake eels

One speckled worm eel (*Myrophis punctatus*) was collected with a dip net in Riceboro Creek under the Seaboard Railroad bridge. The 243-mm specimen was taken at a salinity of 0‰ and temperature of 24°C. Miller and Jorgenson (1969) also reported it from the beach and high marsh habitats.

Three shrimp eels (*Ophichthus gomesi*) were trawled in the lower reach at stations 4, 7, and 9. They probably burrow and easily escape the trawls. I have also seen specimens of the pale-spotted eel (*O. ocellatus*) from the Georgia coast.

ORDER CLUPEIFORMES

Clupeidae - herrings

Three anadromous species of shad (*Alosa*) are listed (Table 2) for the habitats along their migratory route. I collected the American shad (*A. sapidissima*) and hickory shad (*A. mediocris*) only in saline waters. Both of these species and the blueback herring (*A. aestivalis*) spawn in the nearby Altamaha River (Godwin and Adams, 1969).

Young American shad were occasionally collected from the lower reach to the upper reach from December to April. Since the spawning season of the American shad is from March through May in the Altamaha River (Godwin and Adams, 1969), 60- to 114-mm specimens collected from December to March were approximately 1 year old, and a 29-mm shad collected in April was recently spawned. Both age groups were represented in the upper reach but only individuals of age group I were taken in the middle and lower reaches.

Two species and a hybrid of menhaden (*Brevoortia*) (Dahlberg, 1970) occur within the estuary. The Atlantic menhaden (*B. tyrannus*) occurred in eight habitats. Compact schools of adults occurred in the lower reach of the estuary and along the beaches from spring through fall. Smaller numbers were present in the sounds in the winter. Juveniles (29-42 mm) were often collected from June to September in the upper reach where salinity ranged from 0.5 to 16.8‰ and temperature, from 28.4° to 30.8°C. Juveniles were also collected in the oligohaline Riceboro Creek and this species is known to occur in fresh water (Gunter, 1956). Young menhaden (30-99 mm) also occurred in the tidal pools and tidal ditch in May and June.

The yellowfin menhaden (*B. smithi*) was collected in the high-salinity pools, tidal canal, and along the beach. Its absence from trawl collections supports my theory (Dahlberg, 1970) that *B. smithi* is a bay or shallowwater species. The occurrence of this species apparently is restricted by low temperature as it first appeared in May and was present until water temperature decreased to approximately 20°C in November. Its absence after November may result from a southward migration since it is common along Florida in the winter (Dahlberg, 1970).

The hybrid (*B. smithi* × *B. tyrannus*) was the least common of the menhadens. It was collected with *B. smithi* on 5 May 1969 in the tidal canal which had a salinity of 18.8‰ and a temperature of 29°C. Hybrids were collected also along the beach and in the Marine Institute's boat basin at Sapelo Island.

The gizzard shad (*Dorosoma cepedianum*) and threadfin shad (*D. petenense*) are euryhaline species that are important forage fishes in Georgia reservoirs. The gizzard shad is known from the upper reach and the oligohaline creek from two trawl collections made on 19 November 1969. These large gizzard shad (205-220 mm) were collected at water temperatures of 15.5° and 14.1°C, and others were caught in the Marine Institute's boat basin (lower reach habitat) in the summer of 1969.

The occurrence of the threadfin shad at Sapelo Island may have resulted from recent introduction of this species in the Altamaha and Savannah River drainages by the Georgia Game and Fish Commission. Movement to the north through estuarine waters is also possible. This species was taken in water as saline as 29.8‰ and over a temperature range of 26.0° to 30.6°C.

The scaled sardine (*Harengula pensacolae*) and Atlantic thread herring (*Opisthonema oglinum*) were occasionally collected in the higher salinity waters of the beach, lower reach, and high marsh habitats. The Spanish sardine (*Sardinella anchovia*) was reported from St. Simons Beach by Miller and Jorgenson (1969).

Engraulidae - anchovies

Of four species of anchovies known from Georgia, only the striped anchovy (*Anchoa hepsetus*) and bay anchovy (*A. mitchilli*) were common and widely distributed in the estuary. The bay anchovy was one of the most abundant fish species in trawl and seine collections. It was often collected in fresh waters of the oligohaline creek and upper and middle reaches, but was absent from protected waters with low salinity. The bay anchovy was present throughout the year at a temperature range of 7.9° to 32.0°C. The striped anchovy was found in fewer habitats than the bay anchovy, and it occurred only during warmer seasons, May to November, at a temperature range of 15.7° to 30.8°C.

Two tropical species (*A. cubana* and *A. lyolepis*) were collected at St. Simons Beach (Miller and Jorgenson, 1969) but were not collected at Sapelo Beach.

ORDER SALMONIFORMES

Esocidae - pikes

The pickerel (*Esox americanus*) was collected at five freshwater stations. On 16 December 1969, one specimen was trawled in lower Riceboro Creek where the salinity was 0.3‰ and the temperature, 7.4°C.

Umbridae - mudminnows

The little-known eastern mudminnow (*Umbra pygmaea*) was collected at freshwater station 6, the Ogeechee River tributary. This Coastal Plain species is rare in collections from Georgia waters.

ORDER MYCTOPHIFORMES

Synodontidae - lizardfishes

Only one species (*Synodus foetens*) of the lizardfishes ranges inshore in Georgia estuaries. Six specimens were collected by trawls in 1967 and one by a seine in 1969 in the lower and middle reaches from June to November when the salinity was 16.7 to 32.0‰ and temperature was 16.3° to 31.5°C.

ORDER CYPRINIFORMES

Cyprinidae - minnows and carps

Three species of the freshwater cyprinids were collected. Some large carp (*Cyprinus carpio*) were caught in the lower Atlamaha River during the spring and some apparently moved to Doboy Sound and off Sapelo Beach with the flood waters that reduced salinities to 6.8‰ along Sapelo Beach. Three large carp were found dead on Sapelo Beach in April 1970. Some survived in a low-salinity tidal creek that was temporarily dammed on Sapelo Island until June when they were found dead. The alien carp is not known from the North Newport River headwaters.

The golden shiner (*Notemigonus crysoleucas*) was common in the freshwater habitat, and three juveniles (20-24 mm) were collected in the oligohaline creek on 4 September 1969 when the salinity was 0‰ and temperature was 26.4°C. The golden shiner is a common bait and forage fish in Georgia.

The little-known taillight shiner (*Notropis maculatus*) was taken only at freshwater station 4.

Catostomidae - suckers

The lake chubsucker (*Erimyzon sucetta*) was collected at freshwater stations 1, 4, and 6.

ORDER SILURIFORMES

Ictaluridae - freshwater catfishes

Three species of freshwater catfishes were collected. The yellow bullhead (*Ictalurus natalis*) was common in freshwater stations. A 16-mm tadpole madtom (*Noturus gyrinus*) wandered downstream from its typical freshwater habitat to the Crossroads station where the salinity was 1.9‰. The white catfish (*I. catus*) ranged down the estuary to the middle reach (trawl stations 10 and 11) when the salinity was reduced to 11.7 and 9.2‰ and temperatures were 11.1° and 10.8°C, in January and February. White catfish were seined and trawled (10-ft trawl) on nine occasions in the oligohaline creek at salinities less than 1‰ and at a temperature range of 7.4° to 28.4°C. Large samples including specimens over a length range of 40 to 300 mm, trawled in January and February 1970, suggest that large numbers of white catfish moved into the oligohaline creek when temperatures were 8.6° and 10.0°C. The low temperatures could also reduce their mobility and ability to avoid the trawl.

Ariidae - sea catfishes

The sea catfish (*Arius felis*) and gafftopsail (*Bagre marinus*) were most abundant in the lower reach of the estuary but also occurred in the middle reach and beach habitats. Most of the sea catfish (*Arius*) migrated to the ocean in the late autumn and winter and returned to the estuary and beaches in the spring (Table 3). Males orally incubated the marble-sized eggs in June and July. Young with and without yolk sacs were incubated in August until they were 42 mm long or longer. Young lost the yolk sac when they were 37 to 40 mm long. The gafftopsail also is an oral incubator, but none of the few adults collected contained eggs or young. This species is common in the warm months but scarce in the winter.

ORDER PERCOPSIFORMES

Amblyopsidae - cavefishes

The rare swampfish (*Chologaster cornuta*) was collected at freshwater station 7.

TABLE 3.—Length-frequency distribution of the sea catfish, *Arius felis*, collected with a trawl, 1967. There was no June collection.

Length	Apr.	May	July	Aug.	Sept.	Oct.	Nov.
mm							
25-30				4			
31-35				31			
36-40				104	4		
41-45				123	19		
46-50				90	65		
51-55				45	93	8	
56-60				10	72	26	
61-65				2	55	92	1
66-70	1				11	92	2
71-75	1	3		1	3	51	
76-80	3	3			3	22	
81-85	3	5					
86-90	2	24					
91-100		27	2		1		
101-110		7	20				
111-120		1	53		2		
121-130	1		37	16			
131-140		7	7	16	1		
141-150		7	1	3			
151-160		10	8	2			
161-170		2	13	3			
171-180		10	7	8			
181-190		11	3	6			
191-200		11	9	6	1		
200-210		9	5	3			
211-220		5	6	2			
221-230		3	1	2			
231-240		3	2				
241-250		3					
251-260		2					
261-280		2					

Aphredoderidae - pirate perches

The pirate perch (*Aphredoderus sayanus*) was collected at freshwater stations 3, 4, 5, and 7, and one specimen was taken in fresh water in the oligohaline creek.

ORDER BATRACHOIDIFORMES

Batrachoididae - toadfishes

The oyster toadfish (*Opsanus tau*) was often collected in small numbers in trawls in the lower and middle reaches of the estuary throughout the year. This toadfish is sometimes seen in oyster reefs, and one specimen was found in a fouling community on the underside of a floating dock. The collection of only one specimen in the beach habitat can be attributed to the lack of cover. Salinity ranged from 12.4 to 32.0‰ and temperature, from 28.4° to 30.8°C.

ORDER GOBIESOCIFORMES

Gobiesocidae - clingfishes

The habitats of the small skilletfish (*Gobiesox strumosus*) are similar to those of toadfish. It is usually associated with oyster reefs or bottoms that provide cover, especially shell bottoms. The skilletfish occurred in small numbers in the lower and middle reaches throughout the year.

ORDER LOPHIFORMES

Antennariidae - frogfishes

Two species of frogfishes (Table 2) collected at St. Simons Beach (Miller and Jorgenson, 1969) are stragglers from offshore. The sargassumfish (*Histrio histrio*) is often associated with sargassum weed, which drifts onto Sapelo Beach.

ORDER GADIFORMES

Gadidae - codfishes

The southern hake (*Urophycis floridanus*) and spotted hake (*U. regius*) were common in the trawl collections in the lower and middle reaches from January to May. These southern representatives of a group that inhabit cold water first entered the estuary when the temperature was 8.2° to 10.1°C in January, and they remained until it rose to 24.3° to 24.6°C. Salinity and temperature ranges were 12.4 to 30.6‰ and 9.0° to 24.6°C for *U. floridanus*, and 14.5 to 31.1‰ and 8.2° to 24.3°C for *U. regius*. Miller and Jorgenson (1969) also reported four *U. regius* from St. Simons Beach.

Ophidiidae - cusk-eels

This family is represented by one species, the striped cusk-eel (*Rissola marginata*), in Georgia estuaries. Small numbers of this burrowing species were collected throughout the year by trawling in the lower and middle reaches at salinities of 11.6 to 32.6‰ and temperatures of 8.0° to 30.0°C.

ORDER ATHERINIFORMES

Belonidae - needlefishes

Several needlefishes range to the Georgia coast, but only the Atlantic needlefish (*Strongylura marina*) is common in Georgia estuaries. It is occasionally seen around docks in the lower and middle reaches and specimens were seined at the beach, high marsh, and middle reach habitats. Specimens (52-315 mm) were collected from May to October at 22.9° to 30.9°C.

Cyprinodonidae - killifishes

These small fishes are found almost entirely in shallowwater habitats. The euryhaline sheepshead minnow (*Cyprinodon variegatus*) was present throughout the year at salinity and temperature ranges of 0.8 to 34.0‰ and 7.9° to 31.9°C in the tidal pools, beach, high marsh, and tidal canal habitats.

The golden topminnow (*Fundulus chrysotus*) was collected at freshwater stations 3 and 5.

The marsh killifish (*F. confluentus*) occurred at freshwater station 1 and at Crossroads but was common only at an artesian well and in the low-salinity tidal pool where it occurred throughout the year. Recorded salinity and temperature ranges were 0 to 24.4‰ and 7.8° to 29.3°C.

The mummichog (*F. heteroclitus*) occurred at all the habitats except the freshwater habitat. Although it is a shallowwater species, two collections were made at trawl stations (10 and 12) that were close to the marsh. The mummichog was common at most seine stations but was rare along the beach. Recorded salinity and temperature ranges were 0 to 34‰ and 7.8° to 32.2°C.

The southernmost record of the spotfin killifish (*F. luciae*) was reported by Miller and Jorgenson (1969).

The striped killifish (*F. majalis*) was present at the Sapelo Beach throughout the year, but was scarce during the coldest months. It was also common in the high marsh and high-salinity tidal pools, and uncommon in the tidal ditch. The striped killifish was not taken at sand bars in the middle reach although it was col-

lected at low salinities. Salinity and temperature ranges were 6.8 to 34.0‰ and 7.0° to 32.2°C.

The last three cyprinodonts listed on Table 2 are freshwater species characteristic of the Coastal Plain. The bluefin killifish (*Lucania goodei*) is also common in fresh water on Sapelo Island.

Poecilidae - livebearers

The euryhaline mosquitofish (*Gambusia affinis*) occurred at seven habitats and was abundant at the freshwater, oligohaline creek, and low-salinity tidal pool stations. It was collected on the beach only when the salinity was 6.8‰, but it was not uncommon at higher salinities. Salinity and temperature ranges were 0 to 34‰ and 7.3° to 30.7°C.

The least killifish (*Heterandria formosa*) is a freshwater species that occasionally wanders into estuarine waters. The highest salinity record was 4.0‰.

The sailfin molly (*Poecilia latipinna*) was common in the shallow protected waters of the tidal pools, tidal ditch, and an artesian well on Sapelo Island. It occasionally occurred in the high marsh, beach, and oligohaline creek habitats. Temperature and salinity ranges were 7.3° to 32.2°C and 0 to 34‰.

Atherinidae - silversides

The rough silverside (*Membras martinica*) was common at the beach and high marsh habitats. It was attracted to artificial lights at night and collected in large numbers with a dip net in the lower reach. Because of their pelagic nature and small size, only one was collected in a trawl.

The Atlantic silverside (*Menidia menidia*) was found in the four high salinity habitats and in the middle and upper reaches of the estuary. This silverside was common only at high salinities, but it occurred at a sand bar in the middle reach when the salinity was 0.9‰ on 4 September 1969. Although collected at a temperature range of 7.0° to 31.5°C, this silverside left the sand bars of the middle and upper reaches at temperatures below 12°C.

The tidewater silverside (*Menidia beryllina*) was common in the freshwater and oligohaline creek habitats at salinities of 0 to 7.9‰. It ranged to the middle reach when the salinity was 0.1‰. One was collected at Sapelo Beach when the salinity was 6.8 to 7.7‰; this was the only occasion the two species of *Menidia* were collected together although their habitats and salinity tolerances overlap.

ORDER GASTEROSTEIFORMES

Syngnathidae - pipefishes and seahorses

One lined seahorse (*Hippocampus erectus*) was collected by trawl in Johnson Creek (station 4) in May 1969 at a salinity of 27.1‰ and a temperature of 22.3°C. The northern pipefish (*Syngnathus fuscus*) was taken sporadically by trawl and seine throughout the year. It occurred in four habitats at a salinity range of 0 to 31.3‰.

The chain pipefish (*Syngnathus louisianae*) was uncommon in all six habitats where it was found. It was taken by trawl and seine throughout the year, but was less common than the northern pipefish. The chain pipefish was collected only 12 times and at a salinity range of 0.7 to 31.6‰.

ORDER PERCIFORMES

Centropomidae - snooks

The snook (*Centropomus undecimalis*) was represented by young (23-81 mm) collected in protected waters of the tidal pools and tidal ditch. These were collected from June to November at salinity and temperature ranges of 0 to 22.1‰ and 23.0° to 28.6°C. Linton and Rickards (1965) collected 64 juveniles (24.1-74.9 mm long) at Sapelo Island in 1963 and 1964. Their low temperature record of 18°C occurred in November.

Serranidae - sea basses

Of the diverse serranids found on the Georgia coast, only two species range inshore to the estuary. Young of the black sea bass (*Centropristis striata*) and rock sea bass (*C. philadelphica*)

were collected throughout the year in the lower reach, mostly over shell bottoms at trawl stations 3 to 6.

Centrarchidae - sunfishes

Twelve centrarchids (Table 2) were common in the creeks of the Coastal Plain. Six species (*Centrarchus macropterus, Lepomis auritus, L. gulosus, L. macrochirus, L. punctatus,* and *Micropterus salmoides*) were also collected in the oligohaline creek. Although sunfishes have marked tolerance for salinity (Bailey, Winn, and Smith, 1954), none of these were found at a salinity above 0.5‰.

Percidae - perches

The swamp darter (*Etheostoma fusiforme barratti*) was collected only at freshwater stations 3, 4, and 5.

Pomatomidae - bluefishes

The bluefish (*Pomatomus saltatrix*) is often caught by anglers in the beach and lower reach habitats but was rarely taken in this study. Only four young (115-196 mm) were collected, one in each season of the year.

Echeneidae - remoras

A sharksucker (*Echeneis naucrates*) is recorded for the lower reach and beach habitats since one was attached to a lemon shark that was caught from the beach in Doboy Sound (Dahlberg and Heard, 1969).

Carangidae - jacks and pompanos

Nine species of carangids occurred primarily in the beach and lower reach habitats. The horseeye jack (*Caranx latus*) is represented by four specimens from St. Simons Beach (Miller and Jorgenson, 1969). The crevalle jack (*C. hippos*) was occasionally caught by anglers in the lower reach of the estuary and a few juveniles were seined as far up the estuary as the upper reach when the salinity was 10.8‰. Five small specimens (24-77 mm) were collected in the summer and autumn.

The Atlantic bumper (*Chloroscombrus chrysurus*) and leatherjacket (*Oligoplites saurus*) were mostly caught at the high-salinity stations. The lowest salinity recorded for the leatherjacket was 16.8‰. Both occupied shallow waters and the bumper was also caught in trawls.

The lookdown (*Selene vomer*) and Atlantic moonfish (*Vomer setapinnis*) were found in the beach habitat generally from May to November. Lookdowns were occasionally trawled in the sounds.

Young of the commercially important Florida pompano (*Trachinotus carolinus*) and young permit (*T. falcatus*) were common in the beach habitat and occasionally wandered to the high marsh. Young pompano were present from spring to autumn. The palometa (*T. goodei*) was present in summer and autumn at St. Simons Beach (Miller and Jorgenson, 1969), and the permit followed the same pattern at Sapelo Beach.

Lutjanidae - snappers

The gray snapper (*Lutjanus griseus*) spawns offshore, and the young have occasionally been collected in the beach, high marsh, and tidal pools habitats. This primarily tropical species was collected from August to November. The lowest salinity recorded for this species was 13.1‰.

Gerreidae - mojarras

Three species of mojarras, Irish pompano (*Diapterus olisthostomus*), spotfin mojarra (*Eucinostomus argenteus*), and flagfin mojarra (*E. melanopterus*), were collected. The flagfin mojarra was represented in one collection that contained all three species. This unusual collection was at a sand bar in the oligohaline creek on 22 October 1969 when the salinity was 0.7‰ and the temperature was 24°C. The Irish pompano was represented by juveniles collected at six shallowwater habitats. They occurred from July to November at salinities and temperatures of 0.7 to 31.3‰ and 19.4° to 31.8°C.

The spotfin mojarra was collected in seven habitats by seining and was the only mojarra collected (twice) by trawling. This species was

taken from July to November at salinities and temperatures of 0.7 to 31.3‰ and 12.7° to 31.1°C. Dr. C. L. Hubbs identified this species in two collections from Sapelo Beach and Riceboro Creek, and I believe that neither of the closely related species, *E. gula* or *E. jonesii*, occurred in my collections.

Pomadasyidae - grunts

The primarily tropical grunts are represented by the pigfish (*Orthopristis chrysoptera*) in Georgia estuaries. The pigfish was trawled in the lower and middle reaches from June to December and was also collected at the beach. A minimum salinity of 15.4‰ was recorded.

Sparidae - porgies

The sheepshead (*Archosargus probatocephalus*) provides an important sport fishery around docks in the lower reaches and also occurred in the high marsh and beach habitats. The small pinfin (*Lagodon rhomboides*) was rare but widespread (six habitats). Small pinfish (20-87 mm) were present from May to September, and most were collected in the intertidal pools.

Sciaenidae - drums

This is the most important family of fishes in Georgia estuaries to sport fishermen. Sciaenids are the most numerous fishes in terms of numbers available to trawls (Anderson, 1968), and probably most abundant in terms of biomass in trawl collections.

Silver perch (*Bairdiella chrysura*) occupied a variety (8) of habitats. Adults were common only in trawl collections in the lower and middle reaches. The silver perch spawned primarily in April and May (Table 4). The smallest specimens were collected in the lower reach and high-salinity pools in May and June. Two age groups (Table 4) were distinct from May to July. Young grew rapidly from May to October in a wide variety of habitats. They apparently use the whole estuary and also the beach waters as a "nursery ground." Salinity and temperature ranges for this species were 1.3 to 34.1‰ and 7.5° to 32°C.

The spotted seatrout (*Cynoscion nebulosus*) are among the most important estuarine fishes to Georgia anglers. They were occasionally trawled in small numbers in the lower and middle

TABLE 4.—Length-frequency distribution of the silver perch, *Bairdiella chrysura*, collected by trawling and seining, 1967-68.

Length	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
mm												
16-20			3									
21-25			13	6								
26-30			92	6								
31-35			20	14	10							
36-40				8	46							
41-45				1	85	2						
46-50				1	85	8						
51-55				3	66	9	2					
56-60					43	10		1				
61-65					34	15	4	5				
66-70					8	9	7	15		1		
71-75					4	6	7	35	1	2		
76-80						4	13	48	3	2		2
81-85	1		2			4	14	64	5	4	3	5
86-90			1	2		1	14	65	6	5	3	4
91-95	3	7	2	1			6	60	6	4	10	4
96-100	2	1	9	2	1		3	52	4	13	9	1
101-105	1	8	20	5				36	2	8	5	
106-110	4		6	3	1			14			1	1
111-115	2		7		1			4			2	
116-120	1		1		2			1		1		
121-125											1	
126-130											1	
131-135					1							
136-140					1							

TABLE 5.—Length-frequency distribution of weakfish, *Cynoscion regalis*, collected by trawling, 1967-68. None were collected in March.

Length	Jan.	Feb.	Apr.	May	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
mm											
11-20				4	2		2				
21-30				7	42	25	18				
31-40				27	93	66	18	6			
41-50				12	150	55	7	24			
51-60				1	122	24	5	30			
61-70	1				151	17	5	50	1	1	
71-80	1				157	16	9	61	3		
81-90	1			1	141	21	4	56	18	1	
91-100	1				122	28	1	36	24	4	2
101-110	5	1	2	1	95	29		22	18	7	
111-120	1			4	50	41	5	14	5	1	
121-130	1	1	2	11	18	35		9	2	3	1
131-140		1		7	13	25		8	1		
141-150			2	16	6	10		3		1	
151-160				9		4		1			
161-170				3		1					
171-180				1	4	1					
181-190					1						
191-200					1	1					
201-210								1			
211-220								1			
221-230											
231-240		1									

reaches throughout the year. They were rarely seined in shallowwater habitats although many are caught with fishing poles along the beaches and salt marshes. Spotted seatrout are known to spawn in and spend their whole life in the estuary (Tabb, 1966). Juveniles were found as far up the estuary as the upper reach at a salinity of 0.5‰.

During 1967-69, silver seatrout (*Cynoscion nothus*) entered the lower reach of the estuary in May and stayed until July or August.

Weakfish (*Cynoscion regalis*) apparently spawned from April to August (Table 5). With the exception of May samples, age groups are difficult to recognize because of the protracted spawning season. Young weakfish were collected in six habitats. Adults and young were abundant only in trawl collections in the lower and middle reaches. Although most abundant in high-salinity waters, young weakfish occurred at salinities as low as 6.6‰ in the upper reach. Weakfish were conspicuously scarce in the cold months, December to April.

The banded drum (*Larimus fasciatus*) was occasionally collected in the lower reach throughout the year and was collected three times along the beach. It was restricted to high salinities, 22.0 to 34.1‰.

Length frequencies of the spot (*Leiostomus xanthurus*) were based on trawl and seine collections (Table 6). Adults were common in deeper waters and juveniles dispersed to eight shallowwater and deepwater habitats. Young spot (11-85 mm) were among the most numerous fishes of the oligohaline creek where they were collected seven times from April to July at a salinity range of 0.2 to 3.1‰. Young were also common in the tidal pools and tidal ditch. Seine collections indicated that the spot spawned primarily from January to April. Two age groups were distinct from February to May.

The three species of kingfishes (*Menticirrhus*) have marked similarities and differences in their ecologies. All three occurred in the beach and lower reach habitats and were rare in the high marsh. Young southern kingfish (*M. americanus*) were also taken in the middle and upper reaches. It is the only kingfish that was found in low salinities. Four juveniles (19-36 mm) were collected in the upper reach in July and August at salinities of 1.5 to 7.9‰, much lower than the low-salinity limits observed by Gunter (1961).

Seining along Sapelo Beach took young southern kingfish that had been spawned primarily from April to August (Table 7). Young and

TABLE 6.—Length-frequency distribution of the spot, *Leiostomus xanthurus*, collected by seine, 1967-69 (in parentheses) and by trawl in 1967. None were collected in September.

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Oct.	Nov.	Dec.
mm											
11-15		(2)	(3)		(3)						
16-20		(10)	(14)		(2)						
21-25		(6)	(30)	(4)	(1)						
26-30			(12)	(3)	(1)						
31-35				(2)	(6)	(4)					
36-40			(1)	(4)	1 (10)						
41-45				(2)	3 (11)	(2)	(7)				
46-50				(1)	2 (10)		(5)				
51-55				(1)	3 (9)	(3)	2 (9)	(2)			
56-60				(5)	2 (9)	(3)	5 (13)				
61-65				(4)	(5)		6 (6)	(1)			
66-70	4	2			(3)	(3)	7 (3)	1			
71-75	11	10			(1)	(1)	4 (3)				
76-80	12	14			2 (1)	2 (3)	5		3		
81-85	17	12	4		(2)		2 (1)				
86-90	18	14	3				2	1	2 (1)		
91-95	14	18	1	2	2			2			
96-100	19	16	3		4		2	2			1
101-105	23	18	9	2	4		1	2			1
106-110	14	7	7	4	7		1	2			
111-115	21	8	7	2	8			2			
116-120	13	8	11		12		1				
121-125	9	8	7	3	9		1				
126-130	10	5	9	2	10		2	1			
131-135	5	5	10	5	9		2			2	1
136-140	1	2	5	2	9		2				1
141-145	2		4	3	9		5	1		1	1
146-150	2	1		1	4		6			2	3
151-155							7			1	
156-160					1					1	2
161-165					1		2			1	1
166-170							1				

adults also occupied the lower and middle reaches. Although generally common, adults were rare in March and April apparently because they migrate to the ocean where they spawn in offshore waters (Bearden, 1963).

Gulf kingfish (*M. littoralis*) spawned primarily from April to September, judging from 18- to 22-m specimens that were taken along the beach from May to October. The Gulf kingfish was common only along the beach from May to November in my collections.

The northern kingfish (*M. saxatilis*) was the least common of the kingfishes. Young (17-50 mm) occurred along the beach in April and May, and five larger specimens (58-140 mm) were trawled in the lower reach from May to August.

The Atlantic croaker (*Micropogon undalatus*) somewhat resembles the spot (*Leiostomus xanthurus*) in population size and distribution in the estuary. Table 8 indicates that croakers spawned primarily from September to April. Bearden (1964) found that in South Carolina croakers spawned almost entirely in the ocean, and larvae were found from October through May. Young croakers (16-80 mm) were collected in seven habitats, including six shallow-water habitats, at salinities down to 2.7‰. Unlike spots, young croakers were not abundant in shallow water and they did not occur in fresh water. Adult croakers were common in trawl catches in the lower and middle reaches, especially May through August when they were not spawning. The population decline in autumn

TABLE 7.—Length-frequency distribution of the southern kingfish, *Menticirrhus americanus*, collected at Sapelo Beach by seine, 1967-68 (parentheses) and by trawls, 1967.

Length	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
mm												
11-15					1 (4)				(2)			
16-20					1 (33)	(1)	2 (2)	(1)	1 (15)			
21-25					1 (48)	(13)	2 (1)	1 (1)	4 (23)			
26-30					(14)	(24)	19 (14)	21 (2)	11 (7)			
31-35					(2)	(45)	38 (28)	49 (2)	12 (3)	(1)		
36-40						(19)	48 (33)	41	11	6 (2)	1	
41-45					1	(2)	30 (11)	30	5	18	1	
46-50							39 (3)	26	9 (1)	27		
51-55					(1)		15 (1)	28	6	21	2	1
56-60					(2)		15 (2)	29	9	17	3	1
61-65	1				(1)		14	20	8	14	5	1
66-70		2			(1)		15 (3)	21	7	11	3	4
71-75	1	2					16 (2)	12	4	10	8	7
76-80	4	3					19	12	4	7	7	13
81-85	2	6	1				18	16	10	9	6	5
86-90	3	12		1			13	4	4	14	7	4
91-95	4	7					11	9	2	10	6	3
96-100	4	13					7	10	2	5	6	5
101-105	4	6					11	6	2	11	5	2
106-110	1	8	1				1	6	1	6		4
111-115	1	5			2			2	2	10	4	4
116-120	1	6	1		2			1	1	4	5	2
121-125	1	2					1		1	6		1
126-130	1	5			2			1	2	4	2	2
131-135	2				3			2				4
136-140	2	1		1	3		1					1
141-150	3	1	1		4		1	1		3	2	2
151-160	2	1	1		2		2	1		5	2	
161-170	1						2				1	1
171-180	2						2	1				
181-190		1					1	1	1			2
191-200		1			2		3					
201-210	1						1					1
211-220									1			1
221-230										2		1
241-250		1										1

was the result of seaward migration for spawning. Bearden (1964) found ripe croakers 3 to 30 miles offshore. Correlation of movements with spawning is complicated by the protracted (8 months) spawning period.

Large black drums (*Pogonias cromis*) are occasionally caught by fishermen in the lower reach. I collected only a few black drums, all small (19-130 mm), mostly in the high-salinity pools.

The red drum (*Sciaenops ocellata*) is one of the most popular estuarine sport fishes because of its large size and abundance in the beach and lower reach habitats. The red drum was taken in only six seine collections and no trawl collections. The smallest (36 and 37 mm) specimens occurred in November.

The star drum (*Stellifer lanceolatus*) was the most abundant species in the lower reach habitat in 1967 (Dahlberg and Odum, 1970) and also in estuaries near Brunswick in 1933-35 (Anderson, 1968). It is a small species and may account for less biomass than the spot or croaker. Young of the year, apparently spawned from May or June to September (Dahlberg and Odum, 1970), accounted for most of the numbers.

TABLE 8.—Length-frequency distribution of the Atlantic croaker, *Micropogon undulatus*, 1967 and January and February 1968. Most were collected with a trawl. Seine and cast net collections are indicated by parentheses.

Length	1967											1968	
	Jan.	Feb.	Mar.	Apr.	May	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
mm													
16-20											(5)		(1)
21-25					1					(1)	(9)		
26-30					3				1		(6)		
31-35					1				2		(6)		
36-40					2				2	2	(1)		
41-45					3				1	2	2		
46-50		1			10				1		4		1
51-55		2			17	1	1	1		1	1	1	
56-60	1		1		7	1	1	1					2
61-65		2		2	8	5			5			1	1
66-70				1	20	7			11				1
71-75		1		4	17	6			2				
76-80	2	2	1	1	23	13			5	1			
81-85	1			2	25	12	2		8	1	1		1
86-90			1	1	8	18			3	2	2	1	3
91-95			3		7	43	3		5	1	3	3	1
96-100				1	7	47	7		1			2	1
101-105					4	70	6				1	1	
106-110						81	10						4
111-115		1				74	13			1		1	5
116-120		2	1			50	9				2	1	4
121-125	1	1		1		41	10			1		1	1
126-130	1	2				16	5					2	1
131-135		2			1	4	4		1		1		2
136-140						3	3					1	
141-145						3		1					
146-150							1						
151-170								1	1				

Most star drum left the estuary during the cold months.

Kyphosidae and Pomacentridae

These two families were represented only by stragglers from offshore (Table 2). They were collected at St. Simons Beach (Miller and Jorgenson, 1969).

Ephippidae - spadefishes

Small Atlantic spadefishes (*Chaetodipterus faber*) were common in trawls in the lower and middle reaches from June to October at a temperature range of 20.1° to 32.0°C. They were uncommon in shallowwater habitats and were not collected at salinities below 9.9‰.

Mugilidae - mullets

Striped mullet (*Mugil cephalus*) and white mullet (*M. curema*) were widespread and abundant in the estuary. Both species generally occupied shallow water near the surface. The striped mullet was collected in eight shallow-water habitats, and it often enters inland rivers. The white mullet occupied the same estuarine habitats with the exception of the oligohaline creek. This difference may be attributed to salinity preferences since the white mullet was taken at salinities down to 5.0‰ and the striped mullet was often collected at salinities below 0.5‰.

The striped mullet was common or abundant in all the habitats in which it occupied. The white mullet was common in the beach and high-salinity pool habitats. The striped mullet apparently has a greater temperature tolerance since it was collected throughout the year at a temperature range of 7.0° to 31.7°C. The white mullet was absent from collections from January through March and occurred at a temperature range of 15.0° to 32.2°C.

Length frequencies indicated that the striped mullet spawned from September through April and the white mullet from March through September, with some overlap in March, April, and September.

Sphyraenidae - barracudas

Young of two species of barracudas occurred in the beach habitat. One guaguanche (*Sphyraena guachancho*) was collected at Sapelo Beach in October 1967. Three southern sennets (*S. picudilla*) were collected at St. Simons Island Beach in May (Miller and Jorgenson, 1969).

Uranoscopidae - stargazers

The southern stargazer (*Astroscopus y-graecum*) was occasionally trawled in the lower and middle reaches. Young were seined along the beach and in the upper and middle reaches at salinities as low as 12.5‰.

Blennidae - combtooth blennies

Three species of blennies (Table 2) are commonly associated with oyster reefs or patches of oyster shells in the lower reaches of the estuary. The feather blenny (*Hypsoblennius hentzi*) was occasionally trawled in the lower and middle reaches and one crested blenny (*Hypleurochilus geminatus*) was trawled in the lower reach. All three species occasionally occurred along the beach (Miller and Jorgenson, 1969) generally in association with shell or debris.

My data suggest that the feather blenny occurred primarily in deep water in the cold months and that they migrated to the oyster reefs in the warm months where they rear their eggs inside of gaping oyster shells. Three male striped blennies (*Chasmodes bosquianus*), 58 to 64 mm, were rearing embryos inside of gaping oyster shells on 24 April 1970 and 19 May 1970 when water temperature was 27° to 27.5°C.

Eleotridae - sleepers

The fat sleeper (*Dormitator maculatus*) was collected only in the low-salinity tidal pools from May through November in 1967.

Gobiidae - gobies

The lyre goby (*Evorthodus lyricus*) was collected once in the high-salinity pools previous to my collections. All four species of *Gobionellus* were rarely encountered. The darter goby (*G. boleosoma*) was collected three times in the high-salinity tidal pools and was rarely found in the beach or high marsh habitats. Only five specimens of the sharptail goby (*G. hastatus*) were collected—three in trawls, one in the Marine Institute's boat basin, and one in the high-salinity pools. This goby was found only in September 1967 and November 1969.

The freshwater goby (*G. shufeldti*) occurred in the low-salinity tidal pools from May 1967 to February 1968. This goby was also reported in the high-salinity waters of St. Simons Beach and in fresh water of Altamaha River (Miller and Jorgenson, 1969).

The emerald goby (*G. smaragdus*) and green goby (*Microgobius thalassinus*) are two little-known species that were collected only in the high-salinity tidal pools. The former occurred there only in September and November and the latter only in May and November.

Two species of scaleless gobies (*Gobiosoma*) were most abundant in oyster reefs and patches of oyster shells where they laid their eggs inside gaping oyster shells during the warm months. The naked goby (*G. bosci*) occurred in six habitats in addition to oyster reefs and was the most abundant goby in the estuary. It was collected by hand in gaping oyster shells and by seining, and three were trawled. The salinity range was from fresh water to 30.8‰. Only juveniles (18-22 mm) were found at salinities of less than 2‰.

The seaboard goby (*Gobiosoma ginsburgi*) was not collected at regular stations except for specimens from the lower reach that were taken from the stomachs of hakes (*Urophycis*). Males were found rearing embryos inside of gaping oyster shells. On 4 March 1969, a large number of seaboard gobies and a few naked gobies were found in burrows in an eroding clay bank at Sapelo Island Beach.

Trichiuridae - cutlassfishes

The Atlantic cutlassfish (*Trichiurus lepturus*) was occasionally trawled throughout the year in the lower reach but was rare along the beach.

Scombridae - mackerels and tunas

King and spanish mackerels are often caught offshore by sport fishermen during the warm months. Young Spanish mackerel (*Scomberomorus maculatus*) occasionally ranged into the high marsh, beach, and lower reach habitats, but they were rarely collected by seine or trawl because of their speed. One king mackerel (*S. cavalla*) was also collected along the beach (Miller and Jorgenson, 1969).

Stromateidae - butterfishes

The butterfish (*Peprilus triacanthus*) and harvestfish (*Peprilus alepidotus*) are primarily marine fishes that occasionally occur in trawl catches in the middle and lower reaches and in beach seine hauls. They have a wide temperature tolerance as they were collected throughout the year. Butterfish did not occur at salinities below 19.5‰ and harvestfish below 22.8‰.

Triglidae - searobins

Four species of searobins (*Prionotus carolinus, P. evolans, P. scitulus,* and *P. tribulus*) were present in trawl collections in the lower reach throughout the year, and all but *P. carolinus* were trawled in the middle reach. Three of these, excluding *P. evolans,* were occasionally taken in the beach habitat (Miller and Jorgenson, 1969). A salinity of 15.3‰ for *P. evolans* was the lowest I found occupied by searobins. One *P. salmonicolor* was collected in Sapelo Sound.

ORDER PLEURONECTIFORMES

Bothidae - lefteye flounders

The lefteye flounders were represented by eight species that were found only in habitats 1 to 5 (Table 2). Species of *Paralichthys* reach a large size and two of them are important sport and commercial fishes whereas the four other bothids are small. The ocellated flounder (*Ancylopsetta quadrocellata*) and windowpane (*Scophthalmus aquosus*) migrated into the lower and middle reaches during the winter and spring, December or January to May. Water temperature ranges were 8.0° to 26.0°C for the ocellated flounder and 8.8° to 25.7° for the windowpane. These species were seasonally replaced by the bay whiff (*Citharichthys spilopterus*), which was occasionally trawled in the lower and middle reaches from May to October at a temperature range of 26.0° to 31.5°C. Stragglers also occurred in the beach and oligohaline creek habitats.

The fringed flounder (*Etropus crossotus*) was common in trawls in the lower reach throughout the year. There are records from the beach habitat, and a 16-mm specimen was seined in the upper reach when the salinity was 0.5‰.

Two species of *Paralichthys* occur primarily offshore and rarely move inshore. The gulf flounder (*P. albigutta*) was trawled only three times. The broad flounder (*P. squamilentus*) was represented by only one juvenile from the beach habitat.

The summer flounder (*P. dentatus*) and southern flounder (*P. lethostigma*) enter the commercial and sport fisheries of the coast. The summer flounder was most abundant in the lower reach and was rarely trawled in the middle reach. The southern flounder was much more abundant at the middle reach stations than in the lower reach. Its tolerance or preference for lower salinities was also demonstrated by its distribution up the estuary to Riceboro Creek where it was often collected in fresh water.

Soleidae - soles

The hogchoker (*Trinectes maculatus*) is a marine or brackish-water fish that often spends considerable time and travels considerable distances in fresh water. It was common from the lower reach to the freshwater habitat. The hogchoker was present throughout the year in Riceboro Creek where the water was usually fresh.

Cynoglossidae - tonguefishes

The blackcheek tonguefish (*Symphurus plagiusa*) was rarely collected outside of the lower and middle reaches where it was one of the most

abundant species. A low-salinity record of 0.7‰ was obtained from Riceboro Creek.

ORDER TETRAODONTIFORMES

Three marine species (in three families) in this order were represented mostly by small numbers of juveniles. Nearly all specimens were collected in the lower reach and beach habitats. One planehead filefish (*Monacanthus hispidus*) was recorded for a low salinity of 11.8‰. The planehead filefish was in the estuary from April to September at 21.8° to 31.3°C. The northern puffer (*Sphoeroides maculatus*) and striped burrfish (*Chilomycterus schoepfi*) were in the estuary from April to November or December when the temperature was reduced to approximately 11° to 16°C.

LIFE CYCLES OF ESTUARINE SPECIES

Many fishes found in estuaries follow the marine-estuarine life cycle pattern described by Gunter (1967). They spawn in the ocean and the young enter the estuarine and beach waters where the salinity is reduced. The estuary apparently provides them with a nursery ground that is rich in food and a refuge from certain predators, diseases, and parasites that do not thrive in the rigors of highly variable salinities and temperatures. Young of coastal species often have greater tolerance to reduced salinities than adults (Gunter, 1961). Young Atlantic menhaden even require low salinities for development (June and Chamberlin, 1959). Gunter (1967) noted: "The preponderant macroorganisms, both in numbers of species and individuals, are mostly motile species which undergo the general type of life history described above. In southern waters these are the mullet (*Mugil*), menhaden, croakers (sciaenids), shrimp and crabs. Vast numbers of these animals may be found in estuaries at one time or another and in general the very smallest sizes are found in the lower salinities." Some species that spawn in high-salinity waters but were represented predominantly by young in two low-salinity estuarine habitats (oligohaline creek and low-salinity tidal pools) included the spot, striped mullet, hogchoker, southern flounder, ladyfish, tarpon, and snook. The Atlantic menhaden, silver perch, and Atlantic croaker were euryhaline and represented in the upper reach primarily by young.

Since estuaries are being destroyed by pollution, dredging, and filling, it is important to recognize which species are found in estuaries as adults or young. Dependence of the young of marine species on the estuaries is the basis of the nursery ground concept (Gunter, 1967). I expand the nursery ground concept to include all species that are commonly represented by young (defined herein as sexually immature) in estuaries, whether they were spawned in the ocean, estuary, or fresh water.

A total of 168 species is listed for coastal waters (Table 2). The number of species recorded for the estuary is 136 when the numbers of species found only in the freshwater habitat (17) and only along the beach (15) are excluded. The beach and estuary are treated as a single complex here because of their similar fish species compositions. The estuary and beach complex functions as a nursery ground to various degrees for 78 species. Some young sharks and rays that were commonly caught by angling (Dahlberg and Heard, 1969) are included in the compilation. Two species that spawn in fresh water, the anadromous American shad and the white catfish, are also included. The family Sciaenidae includes 13 species that have young dependent on the rich estuarine waters. These sciaenids are the most important group of sport fishes on the Georgia coast and they are potentially important commercial fishes. Atlantic menhaden that are reared in the estuaries are caught offshore in large numbers with purse seines. Vitally important in the food chain are forage species such as the bay anchovy, Atlantic silverside, and rough silverside.

Some organisms that are indigenous to bay or estuarine waters, or at least normally complete their life cycle in these waters, include certain "copepods and planktonic species," several species of molluscs including the American oyster, certain gobioid and cyprinodontid fishes, and a palaemonid shrimp (Gunter, 1967). I have not found fish species that are restricted by salinity tolerances to estuarine waters throughout their

life cycle, but many normally complete their life cycle in the estuary. Some species that typically pass their complete life cycle in the estuary, at least in Georgia estuaries, include those species I later consider to be characteristic of the oyster reefs and certain cyprinodontid fishes such as the marsh killifish, spotfin killifish, and mummichog. The spotted seatrout possibly belongs to this category but adults are common along the beach at times and northern populations migrate offshore in the winter (Tabb, 1966).

There are species that typically complete their life cycle in the ocean or fresh water that are either regular or accidental visitors to the estuary. Another life cycle pattern is exhibited by the anadromous shads (*Alosa*) which spawn in Georgia rivers, including the Altamaha River (Godwin and Adams, 1969). The American eel is the only catadromous species in the estuary.

DIVERSITY OF COASTAL HABITATS

Diversity of habitats is considered here in order to determine the importance of the various habitats to the fish community and also to explore the possible relationship of diversity and stability. A simple index, number of species, is used here in a comparison of habitats (Table 9). To be objective, I define stragglers as those species that are represented by only one collection in a habitat. Further studies would be needed to confidently ascertain which species are naturally rare in their preferred habitats. Discounting stragglers removes a large percentage of the accidental species and makes diversity comparison more meaningful. These diversity values are only roughly comparable because of the differences in sampling effort and gear.

TABLE 9.—Number of species recorded for nine Georgia coastal habitats. To eliminate the influence of stragglers, species recorded (collected or seen) once in the estuary are subtracted from total.

Habitat	Number of species	Species recorded once	Species recorded more than once
1. Beach	114	19	95
2. Lower reach	100	4	96
3. High marsh	56	17	39
4. Middle and upper reaches	61	12	49
5. Oligohaline creek	40	21	19
6. Freshwater creek	39	0	39
7. Tidal canal	22	7	15
8. Low-salinity tidal pool	22	4	18
9. High-salinity tidal pool	37	7	30

The beach habitat produced the highest diversity—114 or 95 species if stragglers are discounted. A high diversity of clupeids, carangids, sciaenids, and bothids accounted for 36 species. Tagatz and Dudley (1961) recorded only 40 fish species from a Beaufort, N.C., beach. Gunter (1958) recorded 44 species from Texas beach station, and Springer and Woodburn (1960) recorded 48 from a beach near Tampa Bay. The latter consider the beach notable for harboring few species compared to other coastal habitats. A low diversity would be expected because the beach offers little niche variety or cover. The higher diversity I report may be attributed to several factors. A large number of species that are typical of other marine and estuarine habitats are occasionally found along the beach. Another factor is the inclusion of eight shark species that were caught while fishing from the beach. A third factor is that Miller and Jorgenson (1969) sampled more extensively than in other studies noted herein. They found 98 species at St. Simons Beach; this total includes 38 species which did not occur at Sapelo Beach.

Species that I consider to be eurythermal in the estuary were collected in both winter and summer and usually in all four seasons, but not necessarily every month. Species that are eurythermal in the beach habitat include the rough silverside (Miller and Jorgenson, 1969), Atlantic silverside, striped killifish, bay anchovy, and striped mullet. Some species that were abundant only in the warm months include the bumper, pompano, white mullet, southern kingfish, and gulf kingfish. Numbers of species and individuals were considerably reduced during the cold months.

The lower reach ranked high in diversity. Most of its 100 species were caught in trawls but seven shark records are based on Dahlberg and Heard (1969). Since only four species are ranked as stragglers, diversity of the characteristic species is similar to the beach habitat. Trawl collections in the region of Cedar Key, Fla., yielded only 63 species (Reid, 1954). This

lower diversity is partially the result of less sampling effort.

Dahlberg and Odum (1970) noted the abundance of species at the 14 trawl stations over the first 14 months of this study. We found that the most numerous species for the first 12 months of the study were star drum (15,209 individuals), weakfish (2,454), blackcheek tonguefish (2,193), sea catfish (1,681), southern kingfish (1,345), silver perch (1,133), bay anchovy (1,090), spot (1,004), Atlantic croaker (896), and spotted hake (467). In shrimp trawl catches in an estuary near Brunswick, 1931-35, Anderson (1968) found the following order of decreasing abundance: star drum, Atlantic croaker, spot, fringed flounder, weakfish, sea catfish, anchovy species, gafftopsail catfish, and kingfish species. In both studies the star drum was the most abundant species. Certain differences (e.g., tonguefish, silver perch, fringed flounder, gafftopsail catfish) may be related to spatial or temporal changes in populations, size of trawl, and mesh size.

Miller and Jorgenson (1969) recorded 56 species, including 39 collected more than once, for the high marsh habitat. Species that were eurythermal in the high marsh also were characteristic of the beach habitat. However, they found the mummichog to be more abundant than the striped killifish in the marsh.

Collections with trawls and seines both contributed heavily to the high diversity (61) of the upper and middle reaches. Some of the species trawled in the middle reach may not occur in the lower salinity upper reach. Species that were eurythermal in the middle reach and common in trawl catches in the middle reach include the Atlantic stingray, bay anchovy, silver perch, spot, southern kingfish, Atlantic croaker, hogchoker, blackcheek tonguefish, and oyster toadfish. Species that were common in trawl catches only during the warm months include the sea catfish, weakfish, star drum, and Atlantic spadefish. Species that were common in trawl catches only during the cold months include the two hake species, spotted seatrout, ocellated flounder, and southern flounder.

Gunter (1967) and others have pointed out that young of marine species are predominant in brackish water. Young fishes that I consider to be eurythermal in the shallow waters (collected by seine, 10-ft trawl, and cast net) of the upper and middle reaches include the Atlantic menhaden, silver perch, spot, southern kingfish, croaker, striped mullet, white mullet, southern flounder, hogchoker, and blackcheek tonguefish. The longnose gar, striped anchovy, bay anchovy, mummichog, tidewater silverside, Atlantic silverside, northern pipefish, and chain pipefish were also characteristic of this region.

The oligohaline section of Riceboro Creek has a low diversity (40 species) especially when the stragglers (21 species) are considered. Tagatz and Dudley (1961) recorded 38 species including 12 freshwater species at an oligohaline station in the Neuse River, N.C. Fishes of the oligohaline creek include 15 freshwater species, 20 euryhaline marine species, 4 anadromous species (*Alosa* and *Dorosoma*), and 1 catadromous species (*Anguilla*). Populations of *Dorosoma* species that occur in saline waters can be considered anadromous as Bailey et al. (1954) have done, but these are primarily freshwater species, at least in Georgia. Characteristic species of the oligohaline creek include the longnose gar, bay anchovy, white catfish, mummichog, mosquitofish, tidewater silverside, bluegill, striped mullet, hogchoker, southern flounder, and spot.

Numbers of fish species decrease up the estuary until the stable freshwater habitat is reached. Most of the 39 species recorded for the freshwater habitat are freshwater species that are characteristic of Coastal Plain waters. Others are migratory or euryhaline marine species, including the anadromous shads (*Alosa*), catadromous American eel, tidewater silverside, northern pipefish, and hogchoker. Fishermen report catching the anadromous striped bass (*Morone saxatilis*) in Riceboro Creek but we have no records.

Miller and Jorgenson (1969) reported 48 species from a freshwater station in the lower Altamaha River. In addition to species that I report, they recorded some marine species, freshwater fishes that usually occur in large rivers and reservoirs, and others that are probably absent from the North Newport River drainage.

The tidal canal and low-salinity tidal pools are

quite similar in diversity and location but some interesting differences exist. The canal is more open to high-salinity water and to the marsh. Larger individuals of some species, such as the striped mullet, silver perch, and spot, entered the canal but not the more isolated pools. The pools contained small species and small individuals of large species. Species characteristic of both habitats include the ladyfish, tarpon, sheepshead minnow, mummichog, mosquitofish, sailfin molly, snook, striped mullet, white mullet, and spot. Species that were restricted to the pools include the marsh killifish, fat sleeper, and freshwater goby.

The greater diversity (37) of the high-salinity tidal pools, compared to the low-salinity pools, is probably related to their higher salinity and greater accessibility from habitats of high diversity (beach and lower reach). As noted previously, salinities and temperatures were similar in the two series of high-salinity pools on the east and west sides of the road to the Sapelo Island lighthouse. Conspicuous faunal differences in the two series of pools may be related to water depth. In the shallow pools of the east side there were large numbers of cyprinodontiform fishes (including the sailfin molly, mummichog, sheepshead minnow, mosquitofish, and striped killifish) and spotfin mojarra. These were all found in much smaller numbers in the deep pool on the west side of the road. The deep pool produced larger numbers of young silver perch, young spot, and gobies. The sharptail goby, emerald goby, and green goby were not found in the shallow pool. Large numbers of striped mullet, white mullet, ladyfish, and bay anchovy were found in the shallow and deep pools.

These semi-isolated tidal pools of estuaries have received little attention in ichthyological studies although they are nursery grounds for many species. Kilby (1955) compared "inner pools" and "outer pools" for two regions on the Florida Gulf coast. He found a higher diversity (36 and 26 species) in the outer pools than in the lower salinity inner pools (19 and 28 species). He did not find significantly more species in open water as I have, because of differences in collecting methods.

The ecological stability of a habitat is generally related to its species diversity. Therefore, it would appear that the low-salinity habitats, tidal pools, and tidal canals would be more vulnerable to pollution than the other habitats. This suggests that locating factories or developments on lower reach or beach habitats would be less likely to damage the fish populations. However, other factors must be considered. For example, the beaches are especially sensitive to development because removal of the stabilizing beach plants results in rapid erosion.

ADDITIONAL COASTAL HABITATS

I consider the oyster habitat to include the oyster reefs of the lower reach and smaller patches of oysters in tidal creeks. The oyster habitat was located near the low tide level and was sampled by hand. Fishes that remain within the interstices between oysters at low tide I consider characteristic. In general order of decreasing abundance, these are: naked goby, feather blenny, skilletfish, seaboard goby, striped blenny, oyster toadfish, and crested blenny. The mummichog was often observed swimming in the vicinity of oysters. At high tide a number of sciaenids migrate to submerged oyster reefs where they provide good fishing. The naked goby, feather blenny, mummichog, and oyster toadfish (one specimen) were also associated with the fouling community on the underside of floating docks in the lower reach.

Few species occur in strictly freshwater habitat on Sapelo Island. Collections were made in a pond at the Marine Institute and ditches at artesian wells. The largemouth bass and bluegill were introduced and are well established in ponds. There are specimens in the University of Georgia Fish Collection of the yellow bullhead and warmouth that were collected on Sapelo Island. These species probably were introduced. Five species that were common in a ditch at an artesian well, locally called Flora Bottom, are the mosquitofish, sailfin molly, marsh killifish, least killifish, and bluefin killifish (*Lucania goodei*). Of these, the first three are euryhaline. The least killifish and bluefin killifish may be native to Sapelo Island, or they could have dis-

persed across the estuary from the mainland since salinities are sometimes reduced to brackish in the estuary.

The stabilization pond of the Interstate Paper Corp. at Riceboro provided a unique study habitat. Fishes were collected on 12 August 1969, 14 April 1970, 2 June 1970, and 6 July 1970. Fishes that were intentionally introduced in 1968 and 1969 and subsequently collected by seining include the largemouth bass, bluegill, and warmouth. Personnel of the paper company also collected adults of the following introduced species: brown bullhead (*Ictalurus nebulosus*) and redear sunfish (*Lepomis microlophus*). I collected four specimens that appeared to be hybrids of the bluegill and redear sunfish. Golden shiners are native to the area but since they were not collected until June and July 1970, they may have been introduced by fishermen. Native species include the mosquitofish, which was abundant, and the least killifish, which was represented by one specimen. I collected juveniles of warmouth, sunfish, mosquitofish, golden shiner, and bass that were spawned in the pond.

DISTRIBUTION PATTERNS OF COASTAL FISHES

The 168 coastal fish species exhibit a variety of distribution patterns in relation to the described habitats. The 86 species that were restricted to one or two habitats included large numbers of (1) freshwater species, (2) elasmobranchs and teleosts that were primarily marine and stenohaline, and (3) rare species. The 30 species that occupied three habitats included only one elasmobranch (*D. sabina*), three freshwater species, and some uncommon and stenohaline species. The large number of species in these categories indicates that a majority of the coastal species occupy only a relatively small number of the coastal habitats. However, the low diversity estuarine habitats (habitats 5, 7, 8, and 9) may be widespread and important nursery grounds to estuarine species that are important as sport, commercial, or forage fishes, e.g., tarpon, anadromous shads, Atlantic menhaden, white catfish, tidewater silverside, silver perch, spotted sea trout, weakfish, spot, Atlantic croaker, striped and white mullets, and southern flounder.

Euryhaline species were defined as species that occur in both fresh water and pure seawater (Gunter, 1956). Although many of the species studied are euryhaline, none were found in all nine habitats. Six species occurred in all habitats except the freshwater habitat, and all of these sometimes occur in fresh water. These widely adapted species are the Atlantic menhaden, mummichog, spotfin mojarra, silver perch, spot, and striped mullet. The mosquitofish, croaker, and white mullet occurred at seven habitats. The mosquitofish was absent from the deepwater habitats. The white mullet and croaker were absent only from low-salinity habitats.

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Mrs. Joyce Swanberg identified representative plants using Radford, Ahles, and Bell (1968) but she used Muenscher (1944) to identify *Elatine*. G. C. Miller identified *Prionotus pectoralis*, now a synonym of *P. salmonicolor*. Dr. C. L. Hubbs identified some *Diapterus olisthostomus*, *Eucinostomus argenteus*, and *E. melanopterus*; Dr. E. Herald, some *Syngnathus fuscus* and *S. louisianae*; Dr. C. R. Gilbert, *Evorthodus lyricus*; and R. W. Heard, Jr., many invertebrates.

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THE RELATIONSHIP BETWEEN THE SUMMER FOOD OF JUVENILE SOCKEYE SALMON, *ONCORHYNCHUS NERKA*, AND THE STANDING STOCK OF ZOOPLANKTON IN ILIAMNA LAKE, ALASKA[1, 2]

STEPHEN H. HOAG[3]

ABSTRACT

The foregut contents of juvenile sockeye salmon in samples taken at night by tow net in the limnetic area of Iliamna Lake consisted primarily of zooplankton and rarely of insects. The number of organisms per foregut was correlated with the estimated zooplankton density between 0 and 100 m. *Cyclops* and *Bosmina* were the dominant zooplankters in both foregut and zooplankton samples. The zooplankton hauls contained a greater percentage of calanoid copepods than the fish foreguts. Food selectivity was indicated but appeared to be minimal. Fry (age 0) foreguts contained a lesser percentage of *Cyclops* and a greater percentage of *Bosmina* than did yearling (age I) foreguts.

Juvenile sockeye salmon (*Oncorhynchus nerka*) spend 1 or 2 years in Iliamna Lake before migrating to sea. They occupy the littoral from the time they emerge from the gravel, in late winter or early spring, until mid-July, when they move to the limnetic area where they remain until migrating to sea in the spring of the following or second year (at age I or age II). A similar change in distribution was found in Lake Aleknagik in the Wood River system (Pella, 1968) and is probably common for all juvenile sockeye salmon in the lakes of Bristol Bay. Preious food studies, summarized by Rogers (1968), indicated that juvenile sockeye salmon feed primarily on insects in the littoral and on zooplankton in the limnetic area.

The standing crop of zooplankton is usually used as an indicator of food availability for zooplankton feeders. However, differences in size, agility, and visibility of the zooplankters may invalidate this assumption.

The objectives of this study were: (1) to determine the food of juvenile sockeye salmon and (2) to compare the composition of the diet with that of the estimated standing stock of zooplankton during the summers of 1966 and 1967. The diets of fry (age 0) and yearlings (age I) were also compared. The population density of juvenile sockeye salmon in Iliamna Lake was high during these years as the escapement into the Kvichak River system was exceptionally large (24.3 million fish) in 1965.

THE ENVIRONMENT

Iliamna Lake is the largest lake in Alaska, with an area of 2,622 km^2 and an average depth of 44 m. It empties into the Kvichak River, which flows into Bristol Bay. The Lake was divided geographically into four sampling areas (Figure 1). Areas I and II have a mean depth of 34 m and an even bottom of glacial till. Area III is much deeper (mean depth 74 m) and has a highly variable, glacially scoured bottom. Area IV is made up of islands and isolated bays and also has a highly variable bottom contour.

Twenty-nine fishes have been identified in the Kvichak River system (Bond and Becker, 1963), but only the sockeye salmon is of commercial importance. The threespine stickleback, *Gasterosteus aculeatus*, the most abundant of the resident species, may compete with the juvenile sockeye salmon for food.

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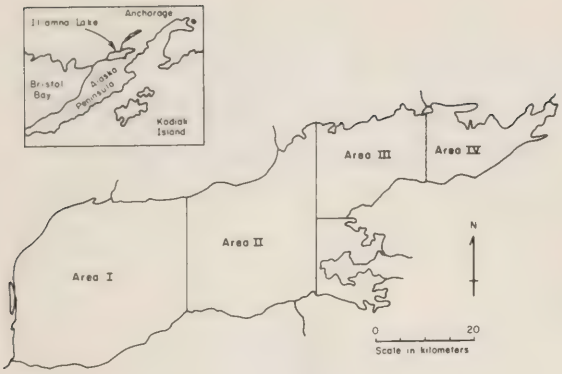

FIGURE 1.—Sampling areas of Iliamna Lake.

The following species of zooplankton occur commonly in the limnetic area of the Lake: *Diaptomus gracilis, Erytemora yukonensis, Cyclops scutifer, Bosmina coregoni, Daphnia longiremis,* and *Holopedium gibberum* (Lenarz, 1966).

Juvenile sockeye salmon and zooplankton exhibit a similar diel vertical migration. Echograms have shown a movement toward the surface at dusk, a concentration usually at less than 10 m at night and a downward movement of fish at dawn. Pella (1968) described a similar diel vertical migration for juvenile sockeye salmon in Lake Aleknagik, Alaska. About half of the zooplankton population occurs above 15 m at midnight and above 50 m at noon in Iliamna Lake (Fowler and Lenarz, 1965).

MATERIALS AND METHODS

Fry (age 0) and yearlings (age I) were collected with a tow net, having an opening of 2.7 m^2 and a cod end mesh size of 0.2 cm, and suspended between two boats spaced 15 m apart with 30.5 m of tow line. Each tow was 20 min in duration at a speed of about 1.5 m/sec. Alternate tows were made at 1.5 and 6 m, and occasionally deeper tows were made when fish were observed at greater depths on the echo sounder. Most samples were taken during darkness (normally between 2100 and 0300 hr). During the day catches were very small at depths of 30 m, and major fish concentrations usually were not seen on the echo sounder. Fishing near the bottom with monofilament, small-meshed gill nets was tried without success.

Fry and yearlings were preserved separately in 10% Formalin within 15 min after capture. No regurgitation of the stomach contents was observed. The fish were measured and the stomachs removed several months later.

The stomach was divided at the major bend, and only the contents of the foregut were examined so that bias from unequal digestive rates among different food items would be minimized. The foregut contents from all the fish in a sample were combined and mixed with water of a known volume. Two subsamples were taken with a 1-ml bulb pipette, and the organisms identified and counted under a low-powered dissecting microscope. Each organism was identified as either *Cyclops, Daphnia, Bosmina, Holopedium,* calanoid copepods, or insects. Nauplii and rotifers were seldom observed and were not counted. The total number of each food item in the sample was estimated by multiplying the number of each food item in the two subsamples by the appropriate factor. The variance between subsamples was less than 1% of the total variance among samples within date and area and was ignored.

The samples ranged from 1 to 45 fish but usually contained between 15 and 25 fish. The results from each sample were weighted by the number of fish per sample and grouped by area and sampling period. The sampling periods were:

1. Late summer 1966 (August 15-September 10).
2. Early summer 1967 (June 20-July 20).
3. Late summer 1967 (August 10-September 5).

The zooplankton sampling (described by Lenarz, 1966) was undertaken for a separate study and differed spatially and temporally from the young fish sampling. Samples were taken with a conical, nylon net of No. 6 mesh attached to a 0.5-m ring by vertical hauls, either from 100 m to the surface or from the bottom to the surface if the depth was less than 100 m. The zooplankters were identified and counted simi-

larly to the organisms in the foregut. Samples were grouped by area and sampling period. The sampling periods were:

1. Late summer 1966 (August 10-26).
2. Early summer 1967 (June 18-30).
3. Late summer 1967 (August 22-September 15).

RESULTS

The numbers of fry and yearlings and the numbers of zooplankton samples by area and sampling period are listed in Table 1. Catches of yearlings in 1966 and of fry in the early summer of 1967 were small and were excluded from the analysis. Both fry and yearlings occurred in varying numbers in nearly all samples during the late summer of 1967. The mean fork length by area and sampling period ranged from 50 to 58 mm for fry and from 71 to 96 mm for yearlings.

TABLE 1.—Summary of samples of fish and zooplankton by area and sampling period.

Sampling period	Area	Age group	Number of fish samples	Number of fish examined	Number of zooplankton samples
Late summer 1966	I	Fry	7	22	9
	II		7	62	9
	III		7	116	6
	IV		17	385	4
Early summer 1967	I	Yearling	7	14	9
	II		8	113	9
	III		7	39	6
	IV		8	81	4
	I	Fry	7	43	9
	II		8	107	9
	III		7	150	6
	IV		7	160	6
Late summer 1967	I	Yearling	8	43	9
	II		8	105	9
	III		7	120	6
	IV		7	90	6
Total			127	1,650	116

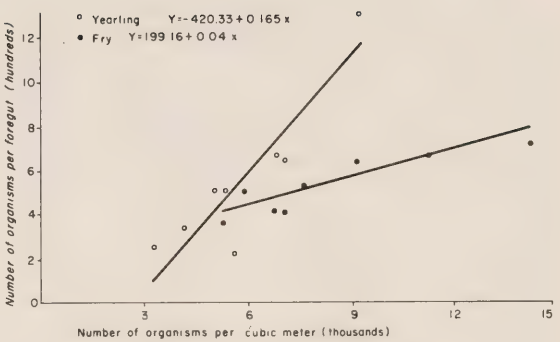

FIGURE 2.—Relationship between the number of organisms per foregut and the number of zooplankton per cubic meter.

FEEDING ACTIVITY

Most juvenile sockeye salmon (94%) contained some food. Temporal and spatial differences in the mean number of organisms in the foregut of juvenile sockeye salmon were apparent although the number of organisms per foregut varied considerably between samples within areas and sampling periods (Table 2). The number of organisms consumed per foregut increased from early to late summer and from area IV to area I.

The mean number of organisms per foregut by age group and the mean number of organisms per cubic meter in each area and sampling period are plotted in Figure 2. The positive slopes, significant at $P = 0.05$, indicate that feeding was in proportion to the abundance of zooplankton. The slope for fry is less than for yearlings probably due to the smaller foregut capacity of fry. Fry probably require a lower food concentration to become satiated, and the number of organisms per foregut may be approaching an

TABLE 2.—Mean number of organisms per foregut and variance between samples by age group, area, and sampling period.

Sampling period	Age group	Area I		Area II		Area III		Area IV	
		$\bar{x}$	s_x^2	$\bar{x}$	s_x^2	$\bar{x}$	s_x^2	$\bar{x}$	s_x^2
Late summer 1966	Fry	715	72,895	685	172,641	525	113,384	502	77,863
Early summer 1967	Yearling	222	46,625	497	157,397	338	8,910	242	50,485
Late summer 1967	Fry	649	66,511	429	31,179	414	20,784	360	35,023
	Yearling	1,323	444,252	680	39,222	660	114,339	496	72,992

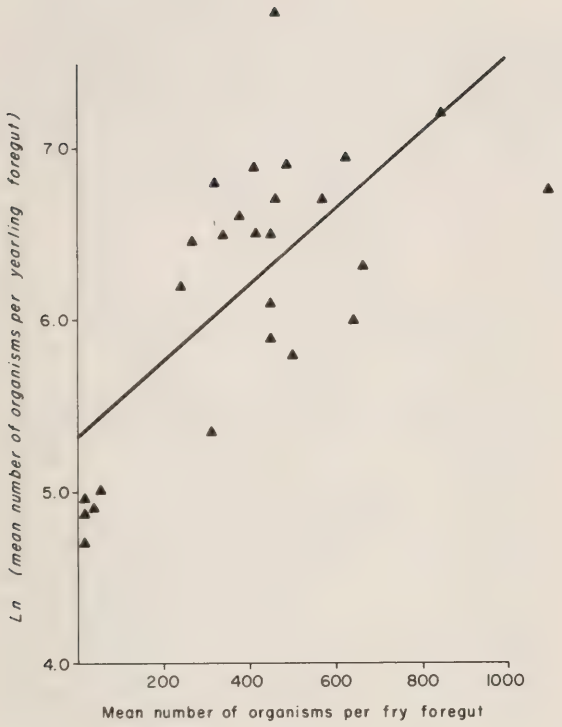

FIGURE 3.—Relationship between the mean number of organisms per foregut in fry and yearlings.

asymptotic upper limit with respect to food abundance in the Lake. The relationship might have been nonlinear for both fry and yearlings if lower and higher zooplankton densities had occurred.

The relationship between the number of organisms per foregut and fish size within each age group was not examined because size range of fry and yearlings in any sampling area was small. However, the yearlings contained an average of 40% more organisms than the fry in the late summer of 1967, probably because of their larger size and feeding capacity. The feeding intensities of both age groups are compared in Figure 3. The correlation coefficient, $r = 0.67$, between the mean number of organisms per fry foregut and the natural logarithm of the mean number of organisms per yearling foregut, significant at $P = 0.05$, indicates an exponential relationship between the feeding intensity of the two age groups. This was expected as fry tend to approach an upper limit of food intake (Figure 2).

COMPOSITION OF THE DIET AND THE ZOOPLANKTON SAMPLES

The food of juvenile sockeye salmon in the limnetic area of Iliamna Lake consisted primarily of zooplankton. Insects averaged less than 1% of the total number of organisms in the foregut except for yearlings from area I during the early summer of 1967, when they constituted 42.6%. *Cyclops* and *Bosmina* were usually dominant in the zooplankton hauls and in the fish foreguts, and averaged 75% in the zooplankton hauls and 90% of zooplankton in the fry and yearling foreguts (Table 3). Yearlings contained a higher percentage of *Cyclops* and a lower percentage of *Bosmina* than fry in late summer 1967 when both age groups were sampled. The percentage of calanoid copepods averaged higher in the zooplankton hauls (13%) than in the fish foreguts (3%) and was consistently higher for all areas and sampling period. *Daphnia* and *Holopedium* occurred in most samples but only constituted 11% of the organisms in the zooplankton hauls and 7% in the fish foreguts.

To compare the percentage composition of organisms in the zooplankton hauls with that of the foregut contents, a "two-way crossed" analysis of variance (fish-zooplankton by area) was performed for each sampling period and for each organism (*Cyclops*, *Bosmina*, and calanoid copepods). *Daphnia* and *Holopedium* were not tested. Mean squares and degrees of freedom are shown in Table 4. The percentage composition of the foregut contents and the zooplankton hauls (Table 3) were significantly different except for *Cyclops* in late summer 1966 and early summer 1967. However, differences in the zooplankton hauls and the foregut contents were not consistent in all areas for *Cyclops* and *Bosmina* as indicated by the significant interaction between the fish-zooplankton samples and areas. Interaction was not significant for the calanoid copepods.

A modification of Tukey's test (Snedecor, 1956, p. 251) showed a significant difference

($P = 0.05$) in the percentage of *Cyclops* and *Bosmina* in fry foreguts, yearling foreguts, and zooplankton hauls in late summer 1967. The percentage of calanoid copepods in fry and yearling foreguts did not differ significantly, but both differed significantly from that in the zooplankton hauls.

Spatial and temporal changes in the composition of the zooplankton catches were compared with changes in the fish foreguts. In the zooplankton hauls, the percentage of *Cyclops* generally decreased and the percentage of *Bosmina* generally increased from early to late summer and from area IV to area I. The composition

TABLE 3.—Mean percentages of *Cyclops*, *Bosmina*, and calanoid copepods in the foregut of fry and yearlings (insects excluded) and in the zooplankton samples by area and sampling period.

Sampling period/ area	*Cyclops*			*Bosmina*			Calanoids		
	Fry	Yearling	Zooplankton	Fry	Yearling	Zooplankton	Fry	Yearling	Zooplankton
	%	%	%	%	%	%	%	%	%
Late summer 1966									
Area I	45.1	--	42.0	45.6	--	38.1	4.0	--	7.1
Area II	29.4	--	41.0	55.5	--	40.9	4.9	--	6.5
Area III	38.1	--	47.5	49.6	--	38.6	1.2	--	6.8
Area IV	26.8	--	62.0	64.5	--	24.9	1.0	--	7.0
Early summer 1967									
Area I	--	58.9	72.4	--	28.9	5.7	--	7.5	13.1
Area II	--	79.0	78.5	--	4.6	3.2	--	1.1	11.0
Area III	--	87.9	84.6	--	4.2	1.2	--	1.7	9.4
Area IV	--	92.3	77.8	--	1.8	1.0	--	4.5	17.9
Late summer 1967									
Area I	21.0	47.2	27.5	68.3	44.0	34.6	2.5	2.3	17.0
Area II	34.6	54.7	14.0	54.3	34.4	45.7	2.3	2.4	16.4
Area III	75.2	84.8	38.4	18.2	6.8	27.0	2.8	2.6	21.1
Area IV	77.6	84.7	36.1	18.0	9.9	23.5	2.3	3.7	24.0
All sampling periods/area	43.5	73.6	51.8	46.8	16.8	23.7	2.6	3.2	13.1

TABLE 4.—Mean squares and degrees of freedom for a "two-way crossed" analysis of variance by sampling period and zooplankton.

	Cyclops		*Bosmina*		Calanoids	
	Mean square	Degrees of freedom	Mean square	Degrees of freedom	Mean square	Degrees of freedom
Late Summer 1966						
Treatments (zooplankton, fry)	65.9	1	644.3**	1	33.0**	1
Areas	117.4**	3	14.0	3	1.5	3
Interaction (treatment × area)	127.7**	3	106.8*	3	1.6	3
Residual	20.6	58	28.1	58	.6	58
Early summer 1967						
Treatments (zooplankton, yearlings)	3.4	1	100.7**	1	166.6**	1
Areas	178.6**	3	109.2**	3	16.8*	3
Interaction (treatment × area)	67.8	3	57.2**	3	5.8	3
Residual	30.8	50	10.6	50	4.8	50
Late summer 1967						
Treatments (zooplankton, fry, yearlings)	1,514.5**	2	615.0**	2	386.1**	2
Areas	1,086.8**	3	887.5**	3	6.0	3
Interaction (treatment × area)	121.0**	6	97.5**	6	3.5	6
Residual	26.9	77	25.0	77	3.5	77

* F test significant at $P = 0.05$.
** F test significant at $P = 0.01$.

TABLE 5.—Rank correlation coefficient (r_d) for percentage of five organisms in fish foreguts and zooplankton hauls by area and sampling period.

Sampling period	Samples	Area			
		I	II	III	IV
Late summer 1966	Fry-zooplankton	0.975***	0.975***	0.800*	0.800*
Early summer 1967	Yearling-zooplankton	.675	.425	.300	.700
Late summer 1967	Fry-zooplankton	.700	.225	.900**	1.00***
	Yearling-zooplankton	.600	—.025	.825*	1.00***

* Significant at $P = 0.20$.
** Significant at $P = 0.10$.
*** Significant at $P = 0.05$.

of organisms in the yearling foreguts showed a similar change; for *Cyclops* and *Bosmina* $r = 0.66$ (significant at $P = 0.10$) and 0.71 (significant at $P = 0.05$), respectively. Correlation was not significant for fry ($r = 0.01$ and 0.22, respectively). The percentage of calanoid copepods in the fish foreguts remained constant in spite of an increase from early to late summer in the zooplankton hauls (Table 3).

Although differences were significant in the percentage composition of organisms in the zooplankton hauls and in the fish foreguts, the fish fed predominantly on those organisms which were most abundant in the zooplankton hauls. Rank correlation coefficients (r_d) were used in comparing the percentage of *Cyclops*, *Bosmina*, calanoid copepods, *Daphnia*, and *Holopedium* in the zooplankton hauls and in the foreguts, and showed very good correlation in several areas and sampling periods and, with one exception, were always positive (Table 5).

COMPARISON OF FRY AND YEARLING DIETS

Cyclops and *Bosmina* were the major food items in the diet of both fry and yearlings although the percentage of the former was greater and the percentage of the latter smaller in the yearling foreguts than in the fry foreguts (Table 3). Differences in the foregut contents may result from slight differences in habitat and hence from differences in available food.

To minimize this possibility only those samples that included at least five fry and five yearlings were examined. The relationship between the two age groups in the percentage of *Cyclops* and *Bosmina* in the foreguts appeared linear (Figures 4 and 5) and a regression analysis was performed. The slope (b) was significantly greater than zero ($P = 0.05$) for both zooplankters; thus, the two age groups have similar food habits. However, the hypothesis $b = 1$ was rejected ($P = 0.05$); therefore, I concluded that fry consume more *Bosmina* and less *Cyclops* than yearlings. The positive intercept in Figure 4 and b less than 1 in Figures 4 and 5 indicate that the percentage of *Cyclops* and *Bosmina* vary less in yearling than in fry foreguts.

DISCUSSION AND CONCLUSIONS

Cyclops and *Bosmina* were the most abundant, and calanoid copepods, *Daphnia*, and *Holopedium*, the least abundant zooplankters in the fish foreguts and in the zooplankton hauls. However, the percentage composition of organisms in fish foreguts differed significantly from those in the zooplankton hauls in that: fry contained more *Bosmina;* yearlings contained more *Cyclops;* fry and yearlings contained less calanoid copepods than the zooplankton hauls.

Discrepancies in estimates of available food and diet are due to sampling error and selective feeding. Spatial and temporal differences in the sampling of zooplankton and fish, and diel and depth variations in available food and feeding activity probably accounted for some discrepancy. Fowler and Lenarz (1965) established diel and depth variations in the percentage composition of the standing zooplankton stock in the lake. Northcote and Lorz (1966) showed diel changes in the food of resident sockeye salmon (kokanee) in Nicola Lake, British Columbia,

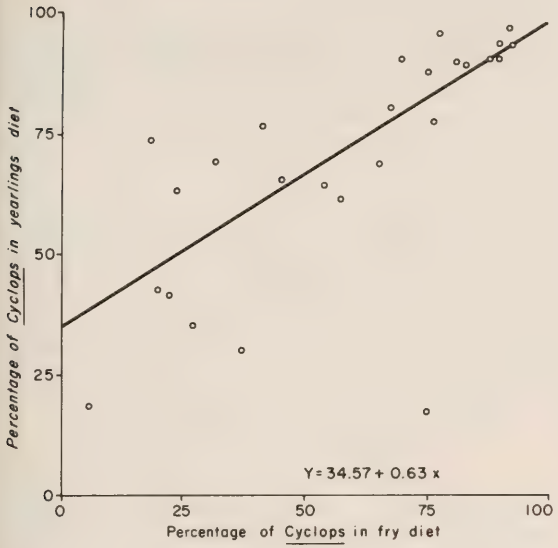

FIGURE 4.—Relationship between the percentage of *Cyclops* in the foregut of fry and yearlings.

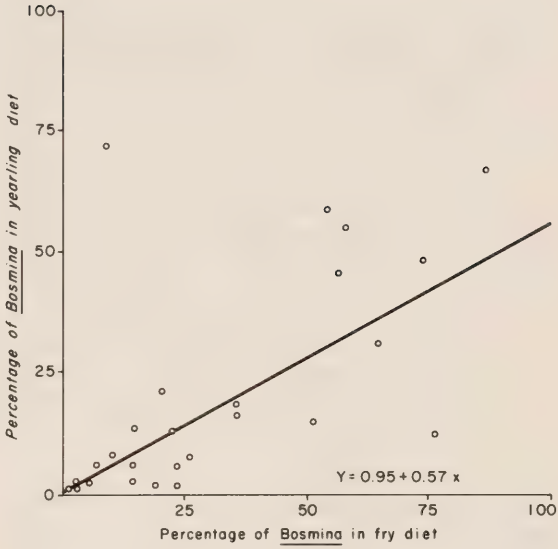

FIGURE 5.—Relationship between the percentage of *Bosmina* in the foregut of fry and yearlings.

and Narver (1970) showed diel and depth changes in the food of juvenile sockeye salmon in Babine Lake, British Columbia.

Food selection depends on characteristics of the feeder and food items (Ivlev, 1961) and probably occurs in some degree for all species. In this study, the cause of the discrepancy between the composition of the foregut and zooplankton samples cannot be attributed specifically either to sampling error or to selective feeding. Whatever the cause, the degree of discrepancy was small, and I concluded that the zooplankton samples generally reflect available food in Iliamna Lake. This is in contrast to Narver (1970), who found that juvenile sockeye salmon strongly selected numerically less abundant zooplankters in Babine Lake.

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SMALL-SCALE DISTRIBUTIONS OF OCEANIC DIATOMS

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ABSTRACT

A sampling study was designed to investigate small-scale abundance fluctuations of diatoms over a distance of 10 miles. It was carried out at three depths in each of two oceanic environments of the North Pacific. Significant nonrandom distributions were observed. The intensity of aggregation varied with species and with depth.

An expression for the approximate confidence intervals for single observations was derived from the 5th and 95th percentiles of the observed frequency distributions.

Statistical analysis of the fluctuations of *Nitzschia turgiduloides* indicated a pattern of distribution with a scale of 1 mile. This may be associated with internal waves in the region of the thermocline.

Knowledge of small-scale distributions of organisms in the ocean is important for evaluation of data based on widely spaced samples, and, hence, is essential for design of efficient sampling programs. Moreover, abundance fluctuations on even the smallest scale relate directly to the ecology of the species, and an understanding of the magnitude and scale of such fluctuations is an important step toward the understanding of a species' relationship to its environment and to other species within its community.

Evidence indicates that the distribution of phytoplankton in the ocean may be highly aggregated (Bainbridge, 1957). A few attempts have been made to sample small-scale aggregations and to investigate quantitatively their density and spacing and the environmental factors which influence them (e.g., Hasle, 1954; Holmes and Widrig, 1956; Barnes and Hasle, 1957; Cassie, 1959a, b, 1960; Bernhard and Rampi, 1965). Although these studies applied a wide variety of statistical procedures to a range of spatial and temporal scales, all of the phytoplankton species studied were reported to have aggregated distributions. However, such studies have all been conducted in the nearshore environments. If, as has been suggested (Cassie, 1957), the contagious distributions of plankton reflect heterogeneities in the environment, then the results of such studies may not be applicable to the more homogeneous environments of the open ocean.

The study described in this paper was carried out in two oceanic environments of the North Pacific. While it was primarily designed to give a quantitative estimate of the precision of samples collected for an extensive study of oceanic diatoms, the results have general interest.

LOCATION OF STUDY

Closely spaced samples were taken twice during Scripps Institution of Oceanography Expedition URSA MAJOR, August-September, 1964. Station 23 (lat 49°07'N, long 155°31'W) was located in the Central Subarctic Pacific and Station 5 (lat 37°00'N, long 155°02'W) in the Central Pacific (Dodimead, Favorite, and Hirano, 1963); both regions were removed from the effects of either neritic environments or the North Pacific Transition Domain. The phytoplankton of the Central Subarctic consisted primarily of diatoms which reached densities in excess of 5,000 cells/100 ml. A total of 27 diatom species was recorded, of which *Nitzschia turgiduloides* comprised 68-92% of the population, and *Denticula seminae* an additional 9-20%. The maximum density of diatoms at the Central Pacific station was only 30 cells/100 ml. The dominant species, *Hemiaulus hauckii*, contributed 20% of the

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total diatom population, and 16 additional species were recorded. Subsequent samples from this region indicated that the major diatom population was below the depth range of the sampling study.

METHODS

At each location a line of stations was positioned with respect to a 10-m drogue. In the Subarctic Pacific, 10 stations were sampled; in the Central Pacific, 11. The stations were spaced at randomly ordered intervals of 0.5, 1.0, and 2.0 nautical miles, covering a total distance of 10.5 miles. At each station samples were collected from depths of 10, 35, and 50 m (wire out).

Samples were collected with 3-liter Van Dorn water samplers. The organisms in samples of 400 ml were preserved with 10 ml of 10% basic Formalin. Aliquots of 50 or 100 ml were settled for 24 hr and the diatoms identified and enumerated under the inverted microscope according to the sedimentation procedure of Utermöhl (1931). The species used for the analysis of distributions were those for which experience has shown the problems of identification and enumeration are negligible. In the case of chain-forming species, the statistical analyses were based upon the numbers of chains per aliquot.

STATISTICAL PROCEDURES

The variance of the cell counts includes the variability introduced into the data during the preparation and enumeration of the subsample, as well as any spatial heterogeneity. If these are independent, the sums of squares will be additive:

$$SS_{total} = SS_{subsample} + SS_{spatial}$$

and the total observed variance is given by:

$$s^2_{total} = SS_{total}/\text{degrees of freedom.}$$

In a brief preliminary study it was demonstrated that, for all species but one, the variability introduced into the data at either the initial or final subsampling stage was no greater than random (Poisson) expectation and may be approximated by the mean count. This agrees with the results of other workers (Holmes and Widrig, 1956; Lund, Kipling, and Le Cren, 1958). The single exception was *Nitzschia turgiduloides*, for which the total introduced variability was $35\bar{X}$.

It has been shown (Venrick, 1971) that the expected total variance of a series of counts from a randomly distributed population is given by:

$$\sigma^2 = \Big\{(n_{al}-1)\,(n_{ss})\,(n_{pop})\,(1-\frac{1}{f_1})\,\bar{X}_{al} + [\,(n_{ss}-1)\,(n_{pop})\,(1-\frac{1}{f_2}) \times (\bar{X}_{al} + \frac{n_{al}}{f_2}\bar{X}_{al})\,] + (n_{pop}-1)\,[\bar{X}_{al} + \frac{n_{al}}{f_2}\bar{X}_{al} + \frac{n_{al}\,n_{ss}}{f_1 f_2}\bar{X}_{al}]\Big\} / [(n_{al})\,(n_{ss})\,(n_{pop}) - 1]$$

where n_{al}, n_{ss}, and n_{pop} are the numbers of aliquots per subsample, the numbers of subsamples per sample, and the number of samples collected from each depth; f_1 is the ratio of sample volume to subsample volume, f_2 is the ratio of subsample volume to aliquot volume; and $\bar{X}_{al}$ is the mean number of cells (or chains) per aliquot. Substituting $n_{al} = 1$, $n_{ss} = 1$, and $f_1 = \frac{3000}{400} = 7.5$, the expression simplifies to:

$$\sigma^2 = \bar{X}_{al} + \frac{1}{f_2}\bar{X}_{al} + \frac{1}{7.5\,f_2}\bar{X}_{al},$$

where $f_2 = 8.0$ for 50 ml aliquots and 4.0 for 100 ml aliquots. For *N. turgiduloides*, the appropriate expected variance is:

$$\sigma^2 = 35\bar{X}_{al} + \frac{1}{7.5\,f_2}\bar{X}_{al}.$$

At each depth, the observed variance, s^2, may be compared with the expected variance, σ^2, and the probability of departure from random expectation determined by means of the ratio

$s^2/\sigma^2 = \chi^2/df$. For 10 and 11 samples $\chi^2(0.05)/df$ values are 1.88 and 1.83 respectively. Species for which the s^2/σ^2 ratio exceeds the χ^2/df value are considered to have aggregated distributions. Ratios greater than 1.63 and 1.60 respectively were significant at the 0.10 level.

With the small number of degrees of freedom involved, the maximum variance attainable by species with mean counts less than 0.2 is too small to give an s^2/σ^2 ratio significant at better than the 0.10 level. For rarer species, a runs test on presence and absence (Tate and Clelland, 1959) was used to give additional information about distribution patterns.

RESULTS

The detection of aggregation in a population is influenced by interaction between volume and spacing of field samples and the scale of aggregation of the population (Grieg-Smith, 1964), and by the proportion of the initial sample which is ultimately enumerated (Venrick, 1971). Thus, the specific results of this study are strictly pertinent only to this sampling design, and they must be interpreted accordingly.

The results of these studies are presented in Tables 1 and 2. Within the Subarctic region, 8 of the 24 distributions were significantly aggregated at the 0.05 level, and two additional species at the 0.10 level. At every depth the species with contagious distributions were the most abundant ones, with the exception of *N. turgiduloides* at 10 m. It is likely that spatial variability of this species was obscured by the large sampling error. Aggregations of the dominant species would result if they had outgrown, in situ, the other species. The fewest aggregated distributions occurred at 10 m. This was the only sampled depth within the mixed layer, and presumably, wind-driven turbulence was sufficient to keep all but the most rapidly dividing species distributed randomly.

Within the Central Pacific, only 3 of the 20 distributions were significantly nonrandom, at the 0.05 level. The runs test, significant at the 0.10 level, indicated that five additional species were aggregated. In this region, aggregation did not appear to be related to the abundance of the species.

Concordance tests were used to investigate the agreement of species with respect to fluctuations of abundances between samples. At Subarctic Station 23 there was significant concordance ($P < 0.05$) between all species at each of the three depths, indicating that species tended to respond to, or be influenced by, their environment in the same manner. In contrast, there was no concordance between species at any depth at Central Pacific Station 5.

PRECISION OF SINGLE SAMPLES

ESTIMATES OF ABUNDANCE

If the frequency distribution of organisms in the field can be fitted to a theoretical distribution, confidence limits on single observations can be derived from the variance of that distribution. Some workers (e.g., Winsor and Clarke, 1940; Barnes and Hasle, 1957) have successfully used logarithmic transformations to normalize abundance data. This procedure was successful for some of the diatom species under consideration in this study. (Normality was tested with normal-probability paper.) The transformation, however, was not successful for all species at all depths and thus a general use of parametric statistics on log-transformed data was not justifiable.

The observed frequency distributions of the aggregated species were satisfactorily predicted by the negative binomial distribution (Anscombe, 1949). Values of k (estimated from the expression $k = \bar{X}^2/(s^2 - \bar{X})$ for the aggregated species ranged from 0.15 to 13.30. The comparisons between the predicted and the observed cumulative frequency distributions were made with Kolmogorov-Smirnov tests (Tate and Clelland, 1959); none were significantly different at the 0.10 level. There are available transformations which normalize negative binomial distributions (Anscombe, 1948). However, these transformations depend upon knowledge of the value of k and thus are applicable only to this particular set of data and not to observations of other species or observations from other environments.

TABLE 1.—Results of sampling study at Subarctic Pacific Station 23.

Species	$\bar{X}_{al}$	σ^2	s^2	s^2/σ^2	P
I. 10-m depth					
Nitzschia turgiduloides[1]	513.5	17,981.23	20,764.30	1.15	--
Denticula seminae[1]	53.8	61.44	271.28	4.42	<0.001
Chaetoceros atlanticus[1]	8.4	9.59	8.26	0.86	-
Dactyliosolen mediterraneus[1]	4.4	5.02	9.30	1.85	<0.10
Coscinodiscus marginatus	2.1	2.40	0.76	0.32	-
Rhizosolenia alata[1]	1.6	1.83	2.26	1.23	-
Thalassiothrix longissima	1.5	1.71	1.16	0.68	-
Rhizosolenia hebetata hiemalis	1.3	1.48	1.56	1.05	--
Corethron criophilum	1.1	1.26	0.98	0.78	--
II. 35-m depth					
Nitzschia turgiduloides[1]	801.0	28,048.62	122,374.22	4.36	<0.001
Denticula seminae[1]	119.3	136.24	1,966.23	14.43	<0.001
Dactyliosolen mediterraneus[1]	23.1	26.38	367.11	13.92	<0.001
Chaetoceros atlanticus[1]	3.0	3.43	17.55	5.12	<0.001
Thalassiothrix longissima	1.5	1.71	3.16	1.85	<0.10
Rhizosolenia hebetata hiemalis	1.4	1.60	2.04	1.28	--
Rhizosolenia alata[1]	0.9	1.03	0.76	0.74	--
Corethron criophilum	0.9	1.03	0.98	0.95	--
Coscinodiscus marginatus	0.8	0.91	1.28	1.41	--
III. 50-m depth					
Nitzschia turgiduloides[1]	330.6	11,581.91	291,104.04	25.13	<0.001
Denticula seminae[1]	39.0	50.04	279.33	5.58	<0.001
Dactyliosolen mediterraneus[1]	7.7	9.88	65.30	6.61	<0.001
Corethron criophilum	0.7	0.90	1.13	1.26	-
Coscinodiscus marginatus	0.6	0.77	0.93	1.21	-
Chaetoceros atlanticus[1]	0.2	0.26	0.40	1.54	-
Rhizosolenia hebetata hiemalis	0.1	0.13	0.10	0.77	--

[1] Statistics based on numbers of chains per aliquot.

The expression which was ultimately chosen to estimate the precision of single observations was derived empirically from the 5th and 95th percentiles of the frequency distributions. For any single count, x, of a nonrandomly distributed species at a single depth, it was found that the expression

$$0.3x \leqslant \bar{X} \leqslant 3.2x$$

included the observed population mean X 90% of the time. The expression was conservative for species with nonaggregated distributions. When all species were considered, the expression included the population mean 95% of the time. The expression gave satisfactory results for estimates of mean numbers of cells of chain-forming species ($P \sim 0.13$) and for mean total diatom abundances ($P \sim 0.14$).

The use of this expression is demonstrated in Table 3, where it has been applied to two samples from 35-m depth at Subarctic Station 23.

TABLE 2.—Results of sampling study at Central Pacific Station 5.

Species	$\bar{X}_{al}$	σ^2	s^2	s^2/σ^2	P
I. 10-m depth					
Hemiaulus hauckii[1]	2.4	3.08	3.45	1.12	--
Asterolampra marylandica	1.0	1.28	1.00	0.78	<0.10 (*r*)
Rhizoselenia hebetata semispina[1]	0.7	0.90	3.42	3.80	<0.001
Asteromphalus heptactis	0.4	0.51	0.45	0.88	--
Chaetoceros dadayi[1]	0.4	0.51	0.45	0.88	<0.10 (*r*)
Nitzschia sicula	0.3	0.38	0.21	0.55	--
Mastogloia rostrata	0.3	0.38	0.41	1.08	--
II. 35-m depth					
Hemiaulus hauckii[1]	1.2	1.54	4.56	2.96	=0.001
Nitzschia sicula	0.7	0.90	0.42	0.47	<0.10 (*r*)
Asteromphalus heptactis	0.6	0.77	0.45	0.58	-
Mastogloia rostrata	0.4	0.51	0.27	0.53	<0.10 (*r*)
Bacteriastrum sp.[1]	0.4	0.51	1.45	2.84	<0.01
Chaetoceros bacteriastroides var.	0.4	0.51	0.45	0.88	--
Chaetoceros bacteriastroides	0.4	0.51	0.45	0.88	--
Asterolampra marylandica	0.1	0.13	0.09	0.69	--
Chaetoceros dadayi[1]	0.1	0.13	0.09	0.69	--
III. 50-m depth					
Nitzschia sicula	0.9	1.15	1.70	1.48	--
Hemiaulus hauckii[1]	0.8	1.03	1.17	1.14	<0.10 (*r*)
Chaetoceros bacteriastroides[1]	0.4	0.51	0.27	0.53	--
Asteromphalus heptactis	0.2	0.26	0.16	0.62	--
Bacteriastrum sp.[1]	0.2	0.26	0.16	0.62	--
Chaetoceros bacteriastroides var.	0.2	0.26	0.16	0.62	--
Asterolampra marylandica	0.1	0.13	0.09	0.69	--
Mastogloia rostrata	0.1	0.13	0.09	0.69	--

[1] Statistics based on numbers of chains per aliquot.
r Nonrandomness indicated only by runs test.

For the more abundant species, the 95% confidence limits which can be placed around a single sample are extremely broad. However, without replicate samples, this interval cannot be significantly reduced. For species represented in a sample by fewer than five cells, the confidence interval given by the empirically derived expression is smaller than that obtained from the assumption of a Poisson distribution. For these rarer species, it is recommended that the confidence interval around a single sample be derived from the assumption of a Poisson distribution (Fisher and Yates, 1957).

ESTIMATES OF DIVERSITY

The variability of individual species in the field determines the precision with which a

single sample estimates the structure of the assemblage. The phytoplankton association within the Subarctic Pacific had a low diversity and significant concordance between species. As a result, the species showed a high degree of consistency of relative abundances within samples. In every sample *Nitzschia turgiduloides* was the numerically dominant species, *Denticula seminae* was the second dominant, and one of two species, *Chaetoceros atlanticus* or *Dactyliosolen mediterraneus* was third in abundance. Thus, a single sample appeared to give a precise estimate of the structure of a less diverse assemblage, even though the large between-sample variability decreased the precision of the estimate of absolute abundances of single species.

In contrast, the phytoplankton association in the upper 50 m of the Central Pacific had a high diversity and lacked concordance between species. At 10, 35, and 50 m, respectively, three, seven, and five species were dominant in at least one sample. Thus, a single sample from a diverse assemblage gave an imprecise estimate of the relative abundances of the component species.

TABLE 3.—Confidence interval about single samples. (95% confidence intervals about single samples, x, calculated from the expression $0.3x - 3.2x$ and compared with the population mean density as estimated by the mean of 10 samples, $\bar{X}$.)

Species		$\bar{X}$	Substation e[1]		Substation h[1]	
			x	Confidence interval	x	Confidence interval
Station 23, 35 m; 50-ml aliquots						
Nitzschia turgiduloides	cells	3,018.0	1,481	444.3-4,739.2	4,654	1,396.2-14,892.8
	chains	801.0	484	145.2-1,548.8	1,252	375.6- 4,006.4
Denticula seminae	cells	395.8	175	52.5- 560.0	624	187.2- 1,996.8
	chains	119.3	87	26.1- 278.4	169	50.7- 540.8
Dactyliosolen mediterraneus	chains	23.1	8	2.4- 25.6	64	19.2- 204.8
Chaetoceros atlanticus	cells	7.7	3	0.9- 9.6	25	7.5- 80.0
	chains	3.0	1	0.3- 3.2	11	3.3- 35.2
Rhizosolenia hebetata hiemalis	cells	1.6	0	-- --	3	0.9- 9.6
	chains	1.4	0	-- --	2	0.6- 6.4
Thalassiothrix longissima	cells	1.5	2	0.6- 6.4	1	0.3- 3.2
Corethron criophilum	cells	0.9	1	0.3- 3.2	1	0.3- 3.2
Total cells		3,491.1	1,704	511.2-5,452.8	5,445	1,633.5-17,424.0

[1] Substations e and h separated by 3.5 nautical miles.

ANALYSIS OF PATTERNS

In the analysis of patchiness and its causal factors, the size and shape of a patch often receives primary consideration. This approach is hampered by the difficulty of accurately defining a patch, particularly where, as in the ocean, one can rarely see the patch as a physical entity. An alternate approach is to examine the scale on which a population shows consistent spatial distribution, regardless of the degree of contagion. Since the detection of nonrandomness depends upon the interaction of the size and distribution of the samples with the population distribution, if the scale of sampling is systematically altered, the observed population variance may change, and those sampling scales which produce maximum variances may indicate scales of heterogeneity in the population distribution.

The six sets of 10 and 11 samples were considered as sets of 45 and 55 pairs of samples separated by intervals of 0.5, 1.0, 1.5, . . . 10.5 miles. For all nonrandomly distributed species, the variance was calculated between each possible pair of samples and averaged for each interval. Thus, for the set of 10 Subarctic samples, in which three pairs were separated by 0.5 mile, four pairs by 1.0 mile, two pairs by 1.5 miles, etc., $\bar{s}^2_{0.5}$ is an average of three variances, $\bar{s}^2_{1.0}$ an average of four variances, $\bar{s}^2_{1.5}$ an aver-

age of two variances, etc. The average variances were plotted against the sampling interval, i.

In the case of one species, *N. turgiduloides*, this technique revealed a periodicity of $\bar{s}_i^2$ with peaks separated by 1-mile increments of the sampling interval (Figure 1 b-d). This indicates a pattern of heterogeneity on a scale of 1 mile which was not apparent from a direct plot of abundances (Figure 1a). The periodicity was best developed at 35 m (runs test significant at $P < 0.001$) where it centered about the population variance, as measured by the total variance of the 10 samples. The periodicity was also highly significant (runs test, $P = 0.01$) at 10-m depth. At 50 m the variance showed significant periodicity ($P = 0.10$) only when the sample from substation h was omitted from the calculation. The high population densities of *N. turgiduloides*, and other species, encountered at substation h were comparable to densities observed at shallower depths, and may represent another scale of patchiness imposed upon the deeper populations by vertical mixing.

The horizontal pattern observed in *N. turgiduloides* was most highly developed along the top of the seasonal thermocline, which, at Station 23, extended between 30 and 50 m. Internal waves travelling along the thermocline produce a regular series of vertical displacements, which may occur on a scale of 1 mile. In species with strong vertical gradients of density at the top of the thermocline, such circulation patterns would produce regular horizontal fluctuations of abundance, such as were observed in the present study. The effect of vertical displacement on the less strongly stratified species may have been obscured by their horizontal variations.

This technique has been successfully used to investigate patterns of terrestrial vegetation (Grieg-Smith, 1964). Once scales of heterogeneity have been defined, those environmental parameters that vary on scales of similar magnitude may be sought as possible determinants of the species patterns. Because this approach is not limited to factors which can be measured simultaneously, it is very flexible. It is applicable not only to parameters in effect at the time of sampling, but also to those whose effect on phytoplankton was exerted some time in the past, and which cannot therefore be directly correlated with abundance. It may for instance prove to be a useful tool for examining the effect of vertically migrating herbivores on the standing stock of phytoplankton.

SUMMARY AND CONCLUSIONS

Of the distributions examined in the present study, less than half showed significant aggregation. For these species the 90% confidence interval about a single sample, x, could be estimated from the interval $0.3x$ — $3.2x$. This expression was conservative for the nonaggregated species.

The inability to establish contagion for the majority of the species investigated in the present study does not prove randomness on this or other scales. However, the prevalence of nonaggregated distributions lends support to the hypothesis that the oceanic environment is less complex than that of the nearshore region. In the oceanic environment, the numerous processes which bring about local variations in abundance of phytoplankton appear to proceed more slowly relative to the randomizing turbulent processes. In such an environment, only the most important local processes produce a measureable effect, and, thus, these may be relatively easily isolated for further study.

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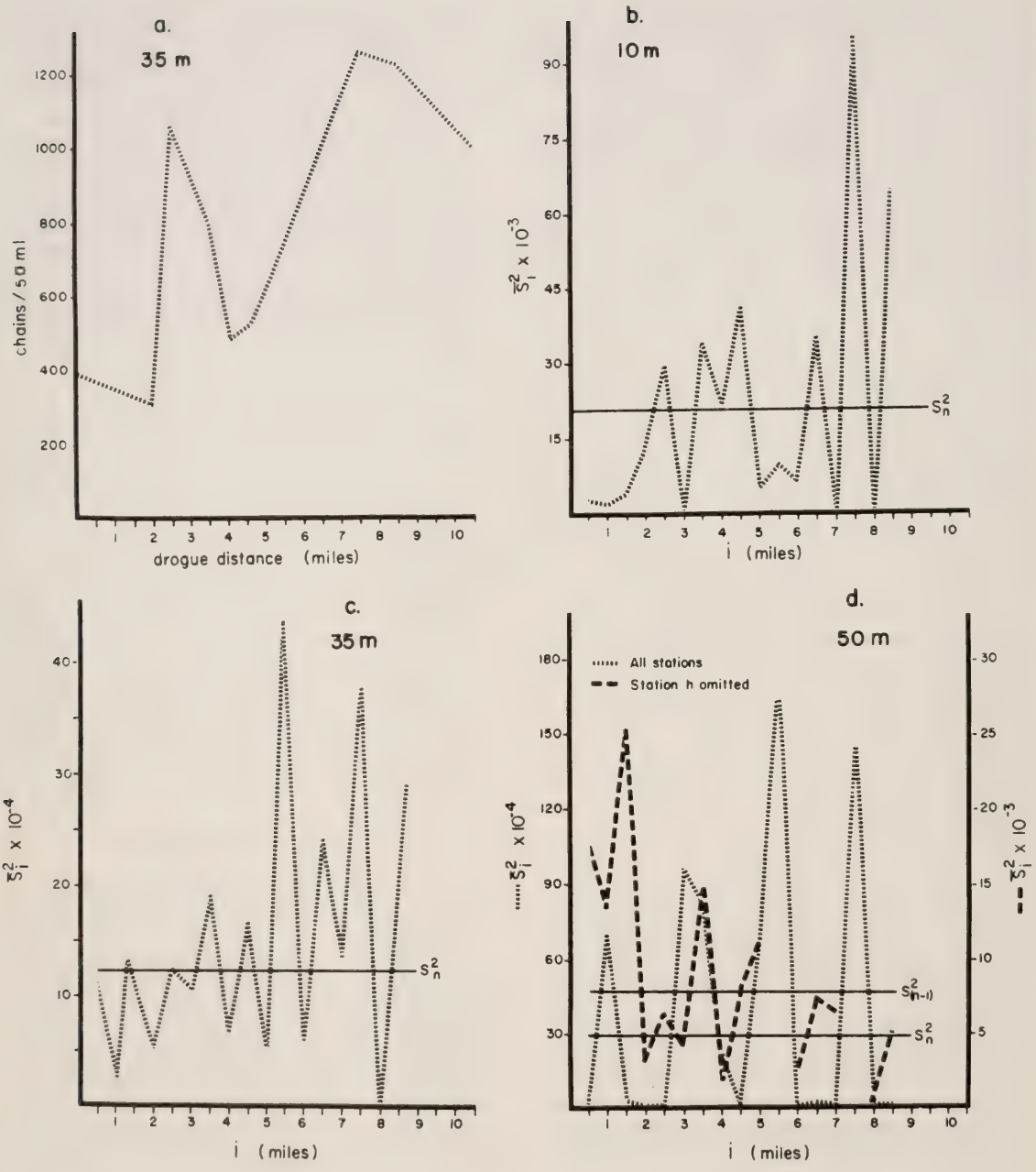

FIGURE 1.—Small-scale distribution patterns of *Nitzschia turgiduloides*. (a) Fluctuations in the abundance of chains, 35 m. (b-d) Fluctuations of the mean, two-sample variance, $\bar{s}_i^2$, with increasing sample interval, i, compared with total variance, s_n^2, of 10 samples: (b) 10 m; (c) 35 m; (d) 50 m; analysis run with (dotted line) and without (dashed line) substation h.

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LABORATORY OBSERVATIONS ON THE EARLY GROWTH OF THE ABALONE, *HALIOTIS SORENSENI,* AND THE EFFECT OF TEMPERATURE ON LARVAL DEVELOPMENT AND SETTLING SUCCESS

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ABSTRACT

The influence of temperature on larval development rate and growth of juveniles of the white or Sorensen's abalone, *Haliotis sorenseni,* was investigated using a thermal gradient apparatus. While larvae developed most rapidly at 20°C, most settled juveniles at that temperature did not survive. At 15-16°C, however, the operculate veliger stage was attained in 72 hr and settlement of advanced individuals occurred in 9 days. No settling was observed at 10°C. Juveniles maintained at 15-19°C and provided mixed diatoms as food showed marked variability in growth rate; at 130 days shell length ranged from 4.0 to 8.0 mm (average 5.5 mm). Two distinctly different patterns of shell pigment distribution emerged with continued growth. Approximately 60% of the juveniles were bicolored, red and yellow-green, while the remainder had an even tone of red-violet.

The description by Carlisle (1962) of the trochophore and early veliger stages of the red abalone, *Haliotis rufescens* Swainson, has heretofore been the only published information on larval development of an eastern Pacific species of *Haliotis.* No account of larval development through settlement and juvenile growth of any of the seven American species of abalones exists in the literature. Details of larval morphogenesis and an estimate of growth during the first year of life for the northeastern Atlantic *H. tuberculata* Linnaeus were given by Crofts (1929, 1937). Japanese workers have reported observations on early development and growth in several of their native species; *H. gigantea* Chemnitz (Murayama, 1935), *H. discus* Reeve and *H. sieboldii* Reeve (Ino, 1952), and *H. diversicolor supertexta* Lischke (Ōba, 1964).

Recent interest in mass culture of commercially important species in Japan and the United States has prompted more critical studies of growth and nutrition of abalones. Advances by Japanese workers in the field of abalone culture were reported by Imai (1967) and Ryther (1968). However, no comparable research information has been published heretofore from any abalone culture facility in California. This work, done in conjunction with abalone culture efforts of California Marine Associates, Cayucos, Calif., describes early growth of the white or Sorensen's abalone, *Haliotis sorenseni* Bartsch.

H. sorenseni exhibits an unusual pattern of distribution. Common to southern California and northern Baja California, it appears in abundance along the mainland only at the northern and southern extremes of its range (Santa Barbara to Pt. Conception and Pta. Eugenia to Pta. Abreojos, respectively). Elsewhere it is islandic, occurring at Santa Cruz, Santa Barbara, San Clemente, Santa Catalina, Los Coronados, and Cedros Islands (Cox, 1962). Adults attain a shell length of about 25 cm and are characterized by an orange-tan epipodium with foliose epipodial papillae, brown cephalic tentacles, and a deeply cupped, light-weight, and scar-free shell. Respiratory apertures are strongly fluted. The species is prized by commercial and sport divers for its white and tender edible portion, the right shell muscle.

Sexually mature *H. sorenseni* have been difficult to obtain in good condition since this is a relatively fragile species and losses in transit

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have been common. On several occasions gravid adults have been retained in our tanks and induced to spawn, but such attempts were never successful in obtaining their larvae. It is considered, therefore, of importance to document a first success with the species.

METHODS

Ten adult *H. sorenseni* were collected at Santa Catalina Island and transported by ship to San Diego, February 18, 1971.[2] Four possessed gonads sufficiently mature to respond to spawning stimuli. Spawnings were induced on February 21 and 26 and March 1, using the thermal shock method (Ino, 1952), but in no case did fertilization occur in greater than about 5% of the eggs liberated. Observations of larval development and growth were carried out with progeny (approximately 1,000 trochophore larvae) obtained March 1 from a single male and female pair.

Fertilized eggs were 190 to 200 μ in diameter. Washing of eggs to remove excess sperm, mucus, and other possibly contaminating substances released during or prior to spawning was achieved by repeated suspension in filtered seawater (Millipore[3] filters, pore size 0.45 μ) following settling and decantation. After incubation of the eggs at 12 $\pm$ 2°C for 24-36 hr, larvae hatched at the trochophore stage. Because the swimming trochophores exhibited a strong negative geotaxis, they concentrated at the surface where they were easily drawn into a Pasteur pipette for transfer to experimental containers.

The effect of temperature on rate of development, settlement, and growth of recently settled juveniles was investigated using an aluminum thermal gradient block (Thomas, Scotten, and Bradshaw, 1963) with compartments bored to accommodate a series of 100-ml beakers. Each compartment could be illuminated from beneath to permit growth of algae within beakers. Containers, arranged in duplicate, were maintained at 10, 12, 14, 16, 18, and 20°C (each $\pm$ 0.5°C). The Pyrex beakers received 80 ml of Millipore-filtered and ultra-violet light treated seawater (Loosanoff and Davis, 1963). Twenty 72-hr veliger larvae were introduced into each together with 1 ml of a suspension of the food organism, *Nitzschia* sp., containing approximately 10,000 cells. To guard against salinity changes due to evaporation or condensation, each beaker was covered with a paraffin sheet, and the entire block insulated with foam styrene. Inspection was made on alternate days to determine the number of larvae surviving, settlement, and growth rate. The water was changed once weekly and new food supplied.

Approximately 500 larvae were distributed among five 1-liter Pyrex beakers at the time the thermal gradient erperiment was begun. These containers received a combination of about 10 species of pennate diatoms collected from illuminated aquarium surfaces in the laboratory (chiefly *Nitzschia, Grammatophora,* and *Navicula*). A thermal environment of 15-17°C was maintained.

DESCRIPTION OF LARVAE

The reader seeking details of morphogenesis in haliotids should refer to illustrations and text as provided for Japanese species by Ino (1952) and Ōba (1964), early development of which closely parallels American members of the genus. In this paper an effort is made to indicate distinctive features of *H. sorenseni* larvae.

Trochophores were subcylindrical in outline, bore a distinct prototroch and were yellow-tan in color. At 15-16°C, the roughly symmetrical shape of the trochophore was soon lost and by 48 hr after fertilization the early veliger form was attained with the incipient cap-shaped shell and lobular velum becoming defined. At 72 hr, the larval shell had taken the typical gastropodan snail-form complete with operculum while shell musculature, viscera, eye-spots, and velum were well developed. At the same time the foot and cephalic tentacles began to differentiate (Figure 1). Tissue pigmentation was predominantly beige, velar fringes were yellow, and the

[2] Collections were made at a depth of about 70 ft by T. Tutschulte and were timed to sample the peak of the reproductive season at the Isthmus station.

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

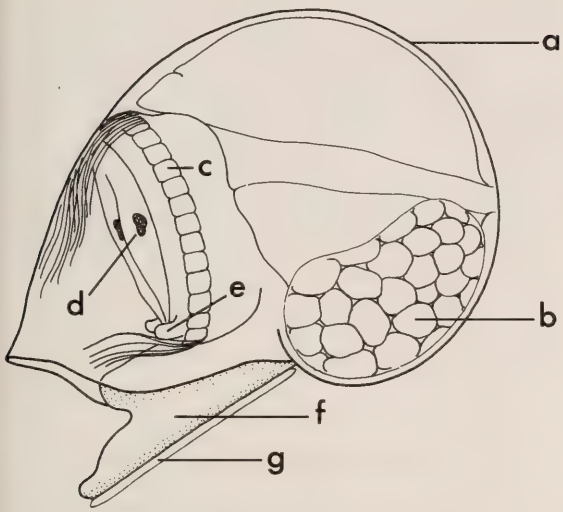

FIGURE 1.—Three-day veliger larva of *Haliotis sorenseni*. (Shell diameter, 270 μ) a. shell, b. digestive gland, c. velum, d. eye spot, e. incipient cephalic tentacle, f. foot, g. operculum.

digestive gland was maroon. Swimming of veligers at this stage carried them throughout the water column.

Settlement occurred at 9-10 days at 15°C. Velar dystrophy, with loss of ciliated fringes, took place gradually, and larvae retained the ability to swim if dislodged for several days after initial settlement.

INFLUENCE OF TEMPERATURE ON DEVELOPMENT RATE

Larvae confined to 100-ml beakers in the thermal gradient block appeared, except for the temperature effects to be described, to be normal in appearance and behavior and were similar to larvae maintained in liter beakers at 15-17°C. Development was most rapid at higher temperatures; some individuals settled as early as the 7th day at 20°C and the 8th day at 18°C. By the 15th day almost all larvae at the two highest temperatures had settled, yet none had settled at 10°C (Table 1, Figures 2 and 3). By the 25th day most larvae at 10°C had succumbed, having progressed only to the late veliger stage. Settling rate varied within groups, and even at 18°C approximately 5% did not settle.

Observations at the end of the 36-day experiment revealed that survival was best at 16° and 18°C, somewhat less at 20° and least at 14° and below. Larvae maintained at 10°C did not survive beyond 25 days and most of those at 12° failed at 25 to 30 days. Size attained by settled juveniles corresponded with survival; at 36 days shell lengths as great as 1.2 mm were attained at 18°C, about 1.0 mm at 20° and 16°C, and only 0.6 mm at 12° and 14°C.

GROWTH OF JUVENILE *H. SORENSENI*

Approximately 100 settled juveniles were obtained from the larvae reared in liter Pyrex beakers at 15-17°C. These individuals were carefully dislodged by a jetting stream of water and teasing needle and transferred to larger containers to observe growth and behavior under a variety of food and water flow situations. Food quality and quantity was not limited to insure maximum growth, hence a wide variety of food organisms was provided (pennate diatoms and filamentous red, green, and brown algae).

TABLE 1.—Number of *Haliotis sorenseni* larvae surviving and settled at 15 days in thermal gradient experiment.

Temperature	Series I			Series II		
	Surviving	Settled	Survivors settled	Surviving	Settled	Survivors settled
°C ± 0.5°	*No.*	*No.*	*%*	*No.*	*No.*	*%*
10	5	0	0	18	0	0
12	7	4	57.2	15	10	66.6
14	15	11	73.4	18	14	77.7
16	12	11	91.5	14	11	78.5
18	9	9	100.0	17	15	88.4
20	7	7	100.0	13	11	84.6

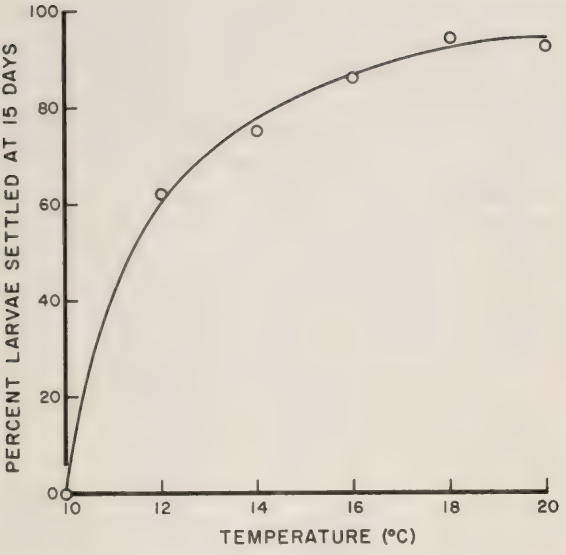

FIGURE 2.—Percentage of larvae firmly settled at 15 days. Points are averages for duplicate observations. Settlement was considered complete when larvae could no longer be dislodged by jetting a stream of water from a pipette.

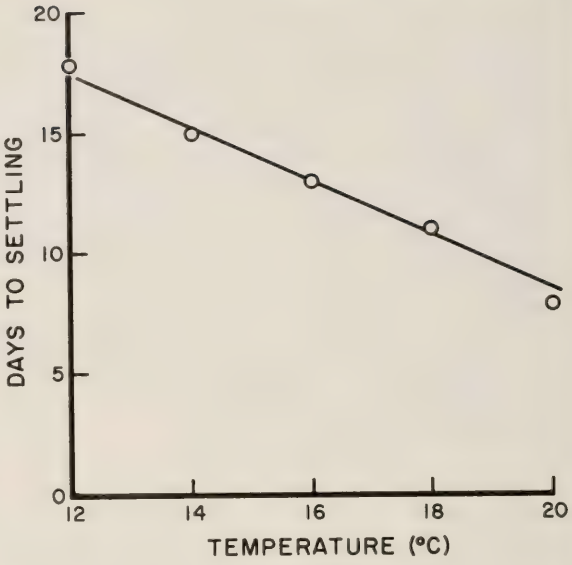

FIGURE 3.—Days to settlement of at least 75% of *Haliotis sorenseni* larvae from groups held at five different temperatures. Not more than 75% of the larvae at 12°C successfully settled, and none of those at 10°C reached this stage.

A marked variation in growth rate existed, even among those individuals which were provided surfaces (such as plastic and glass beakers) on which diatom growth appeared to be quite uniform. In one case, 19 individuals were retained in a liter beaker and provided mixed diatoms. At an age of 85 days some had attained a shell length of 4.5 mm while others were as small as 1.4 mm. The largest had formed four respiratory pores, yet the smallest was just beginning to form the first. Size attained at 100 days (15-19°C) ranged from 3.0 to 5.6 mm (mean, 4.25, SD $\pm$ 0.63 mm, $n = 19$). By 130 days the range was 4.0 to 8.0 (mean, 5.53 mm, SD $\pm$ 1.01 mm) in the same group (Figure 4).

DESCRIPTION OF JUVENILE SHELL FEATURES

The most conspicuous feature of recently settled and minute haliotids (less than 500 μ long) is the asymmetrical outline resulting from dextral growth of the persistomial shell. Through

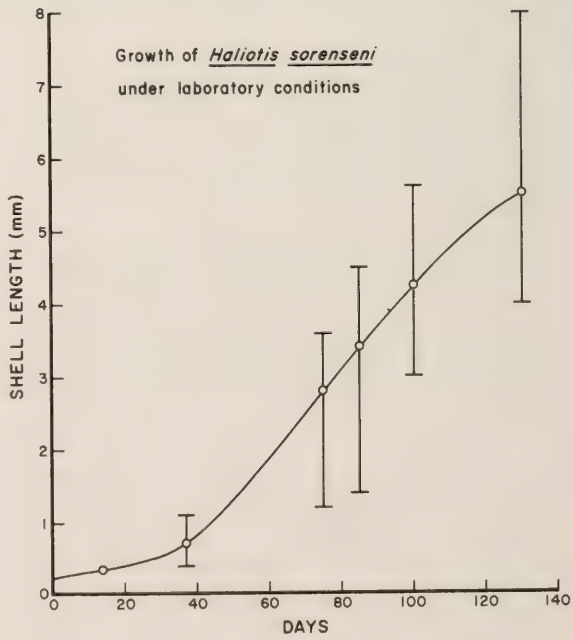

FIGURE 4.—Growth of larval and juvenile *Haliotis sorenseni* in 1-liter beakers provided mixed diatoms as food. Ranges of shell length are shown by vertical lines.

continued growth the asymmetry is reduced and the shell form, as viewed from above, is almost circular until the "notch stage" is reached. Formation of the first respiratory aperture is initiated by separation of two portions of the mantle at the right anterior margin interrupting otherwise uniform marginal shell deposition. The "notch" so formed is a convenient growth mark, reached by the most rapidly growing *H. sorenseni* at an age of 55 days and a shell length of 2.0 or 2.1 mm (Figure 5).

In the juvenile *H. sorenseni* observed, shell pigmentation was a pale violet-pink becoming more vivid as the notch stage was approached. In most cases a cyan-blue flare spread from the apex to the right shell margin. After completion of the first respiratory pore, a dichotomy in pigment pattern emerged. Although all juveniles developed from eggs of a single female, fertilized by a single male, approximately 40% developed an even red-violet shade throughout the greater extent of the shell while the majority became increasingly bicolored with growth. The bicolored pattern consisted of a rich red zone along the left edge of the shell (extending to the aperture row) and pigmentation of blue, green, and yellow over the broader surface right of the aperture row. In individuals of both coloration patterns, a conspicuous ivory-white patch remained at the position of attachment of the right shell muscle until obscured by nacre deposition at about 8 mm. The apex, in turn, became increasingly white.

Elevated apertures, typical of the species, appear even in first-pore individuals. More conspicuous is the ridge bordering the left shell margin. It is this ridge that forms the sharp corner and relatively straight left anterior margin (Figure 6).

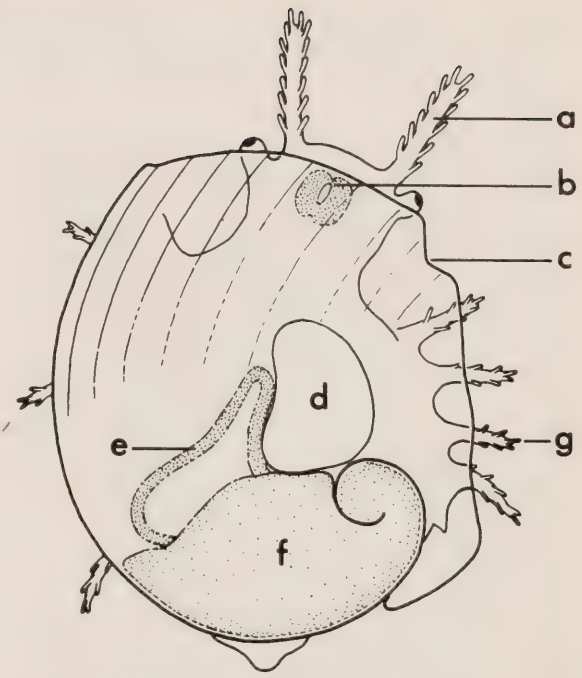

FIGURE 5.—Juvenile *Haliotis sorenseni* at "notch" stage (2.0 mm, 55 days). Shell is still slightly transparent and prominent anatomical features are readily seen from the dorsal aspect. a. cephalic tentacle, b. mouth, c. indentation at point of formation of first respiratory pore ("notch"), d. right shell muscle, e. intestine, f. digestive gland, g. epipodial tentacle.

DISCUSSION

Establishment of specific characteristics by which larvae and juveniles of the seven cooccurring California species of *Haliotis* may be distinguished must await results of studies of fine structure of larval shells. Examination by scanning electron microscope has revealed sufficient detail of fine crystalline and basement structure of larval shells in certain other prosobranchs (Fretter and Pilkington, 1971). Gross shell morphology alone is inadequate to differentiate larvae of even distantly related species. Pigmentation of velar and visceral portions may provide distinctive features for recognition of some species.

Pigments derived from parental yolk appear to be retained by trochophore and veliger larvae of *Haliotis*. Among California species, ovarian tissue is dark green in *H. rufescens, H. cracherodii, H. walallensis,* and *H. kamtschatkana assimilis*. Correspondingly, larvae of these species are conspicuously green. The remaining three species found locally, *H. fulgens, H. corrugata,* and *H. sorenseni,* produce eggs of brown, olive, and beige color, respectively. Their larvae

may be expected to reflect these pigments accordingly. I have examined larvae of *H. fulgens* which were generally brown but with green velar margins and those of *H. sorenseni*, which, as described above, were beige with yellowish velar margins. Tissues of larval *H. corrugata* are light yellow-green while velar fringes are a darker shade of green.

Color of the digestive gland in planktotrophic prosobranch larvae has been shown to reflect diet (Fretter and Montgomery, 1968). Since *Haliotis* veliger larvae are lecithotrophic, color of the digestive gland may have diagnostic value. The maroon-colored digestive gland of *H. sorenseni* veligers appears to be distinctive; I have not observed other than green or brown in the digestive glands of other haliotid veligers.

Although development of larvae and growth of settled juvenile *H. sorenseni* were more rapid at higher temperatures, survival was reduced at 20°C. More advanced juveniles, reared initially at 15-20°C, did not appear adversely affected by temperatures as high as 25°C. Possibly thermal tolerance limits are more restricted in larvae and recently settled individuals. Certainly other factors could have influenced success at higher temperatures. Despite weekly changes of water, bacterial, algal, and protozoan growth together with a build up of metabolites and reduced oxygen tensions in the relatively small volume of water used in the thermal gradient study could have influenced the results.

Larval *H. sorenseni* were not successful at 10-12°C. Water temperatures within the bathymetric range of the species may fall to 12° and occasionally to 11°C (e.g., at depths of 130 ft off Santa Catalina Island, T. Tutschulte, personal communication). Therefore the 10° or 12°C bathyisotherms may limit the depth to which larvae of *H. sorenseni* may successfully settle and grow. The results of the temperature block study indicate the range 14-18°C may be optimal for *H. sorenseni* larvae—an outcome not unexpected in view of the prevailing conditions in the natural environment from Pt. Conception to central Baja California.

Information on growth throughout the first days of life is available for several species of *Haliotis*. Ino (1952) reported that *H. discus* attained only 1.25-1.40 mm at 100 days and that the first respiratory pore was not formed until 130 days. In contrast, Ōba (1964) observed rapid early development of *H. diversicolor supertexta*. In that study, trochophores hatched at only 6 hr, veligers developed within 11 hr and settled by 2 days. The first respiratory pore was formed as soon as 23 days after fertilization. Interpolating from his growth curve, 100-day juveniles ranged from 8 to 13 mm (Ōba et al., 1968). In Ino's study, water temperatures declined from 18° to 10°C through the course of observations while Ōba's work was carried out during the summer and fall when temperatures ranged between 20° and 28°C. Whether the different development rates in these two species reflect specific contrasts or thermal influences is not clear. In another study (Kan-no and Kikuchi, 1962), *H. discus hannai* was reared at a relatively constant intermediate temperature (19-20°C). This species also exhibited rapid early development, settling in 3 days. Juveniles reached 11 mm in length at 100 days and 26 mm at 180 days.

The rather extreme variability in growth rate observed in *H. sorenseni* has also been found in *H. rufescens* (Leighton, unpublished data). Comparable variability is reflected in Ōba's growth curve for *H. diversicolor supertexta*. Differences in growth rate may reflect variation in food availability. In the present study, care was taken to provide uniform food distribution and feeding conditions. Yet within a single container, even within sampled subareas, a full spectrum of size variation could be found. The hypothesis may be advanced that gametogenic inequalities (e.g., yolk allotment) may be involved giving greater advantage to some individuals over others. Indeed, mortalities were more common among the smaller and presumably less active members.

Inherent variability in growth rate may be expected in nature to be complicated by differential quality and availability of food. Multimodal size-frequency distributions obtained for juvenile *Haliotis* populations in the field have been concluded to reflect multiple spawnings and recruitment waves (Leighton and Boolootian, 1963; Boolootian, Farmanfarmaian, and Giese,

FIGURE 6.—Photograph of shells of juvenile *Haliotis sorenseni* representing the bicolored (above) and red pattern (below). Shells range in length from 6.6 to 8.4 mm.

1962). The evidence from this study suggests the assumption of uniform growth within a population of juvenile *Haliotis* is untenable and that conclusions regarding settlement date estimated from sizes of members of a sample must be drawn cautiously.

ACKNOWLEDGMENTS

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EXPLOITATION EFFECTS UPON INTERSPECIFIC RELATIONSHIPS IN MARINE ECOSYSTEMS[1]

SAUL B. SAILA AND JAMES D. PARRISH[2]

ABSTRACT

Due to man's continuing efforts to extract greater harvests of marine organisms from the world ocean, it is becoming increasingly important to be able to predict the consequences of exploitation on complex assemblages of organisms. These assemblages, or ecosystems, consist of predator and prey organisms in various interacting combinations. Preliminary evidence available from studies of marine invertebrate communities in coastal areas has indicated that removal of grazing herbivores or predators at various levels results in lower species diversity and greater instability of the ecosystem. In order to permit a quantitative evaluation of the effects of various rates and types of exploitation on interspecific relationships, model ecosystems were constructed utilizing a subset of graph theory as applied to network analysis. A basic ecological trophic unit was formulated, and these units were combined to form more complex model ecosystems. In particular, a hypothetical four species system of interacting predator and prey organisms was analyzed to demonstrate the consequences of varying certain model coefficients, especially rates of exploitation. It was shown that nonselective exploitation tended to maintain stability of the system better than highly selective exploitation. A hypothetical example of an empirical approach for examining changes in community structure was also demonstrated.

Much of the present theory of fisheries science as well as many practical fisheries management techniques are based on the concept of a single species or unit stock (Beverton and Holt, 1957; Ricker, 1958). This approach continues to be useful in describing and predicting the behavior of fisheries consisting primarily of a single species. Recently, Walters (1969) developed a deterministic computer simulation model for determining optimum harvest strategies based on a unit stock. However, modern fishing seems to be progressing toward exploitation on many species of the larger animals in aquatic ecosystems. To some extent this is due to the tendency toward reduction to meal of many species of fishes. Some obvious areas for the future development of marine fisheries will be in tropical or subtropical waters, such as parts of the Indian Ocean as well as the southeast and southwest Atlantic. These areas are characterized by a relatively greater diversity of species than the traditional fishing grounds of north-temperate regions. It can reasonably be expected that some species will be exploited intensively from them. It therefore seems desirable to attempt to better understand trophic relations of ecosystems consisting of several interacting species in order to develop management techniques for these systems. This increased understanding includes the effects of various kinds of exploitation strategies as well as environmental perturbations on these ecosystems. It is suggested that stresses applied to ecosystems may produce somewhat similar effects, regardless of their origin.

Some of the large volume of literature concerning diversity and stability in terrestrial as well as aquatic ecosystems has been reviewed at a recent symposium (Woodwell and Smith,

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1969). One of the generalizations which appeared to emerge from the symposium was that ecosystems characterized by high species diversity tended to be relatively stable. Elton (1958) has shown that if a predator has several alternate prey species to utilize, it will persist even if one of the prey becomes very scarce. Thus, it seems as if there is some correlation between diversity and stability.

In the case of marine invertebrates, there is some observational evidence (Paine, 1963) to indicate that marine predators at high levels in the food chain feed on more species of prey than do those on lower levels. Observations, such as the above mentioned, have led some ecologists to suggest that high level predators might contribute more to community stability than the lower level predators.

Removal of predators from rocky shore invertebrate communities (Paine, 1966) resulted in a reduction of the species diversity of the animal community. In addition, removal of grazing herbivores from rocky shores has resulted in the rapid growth of some of the formerly eaten plant species and a change in community composition toward lower species diversity (Jones, 1948; Southward, 1964; Paine and Vadas, 1969). The observations and experiments of Paine (1966) also indicated that diversity among competing species of marine invertebrates could be decreased by removal of predators in some instances. A theoretical dynamic analysis (Parrish and Saila, 1970) of a trophic subweb using Lotka-Volterra type interactions offered some support to Paine's conclusions.

With the exception of some pioneering conceptual work by Larkin (1963, 1966) in describing models for interspecific competition and exploitation applied to natural fisheries, very little seems to have been done in an effort to predict the effects of man's activities on aquatic communities consisting of several interacting species. One of the reasons for this appears to lie in the degree of complexity required to establish and express all the basic interrelationships in such a system (Mann, 1969). Recently, Menshutkin (1969) suggested graph theory as a useful tool for minimizing some of the difficulties of constructing models of interacting systems if certain simplifying assumptions, such as linearity and steady-state conditions, could be tolerated. Recognizing that any set of mathematical equations represents at best a crude approximation of the actual behavior of complex ecosystems and that empirical values of coefficients for complex models are largely unavailable, we have proceeded under the assumption that the simplest models should first be explored and carefully evaluated before proceeding to more elaborate formulations. In addition, it is believed that the simplicity of the methods described herein may enhance their utility, especially when considering the initial effects of exploitation or environmental modification on interacting ecosystems.

The objectives of this work were to: (a) introduce a subset of graph theory as used in network analysis; (b) describe a graph theoretic formulation of a basic ecological trophic unit, and to demonstrate some effects of predation and exploitation on model ecosystems consisting of these units; and (c) demonstrate some other uses of graph theory with a view toward stimulating further interest in its applications.

BACKGROUND AND DEVELOPMENT

By definition, a graph is a set of vertices (nodes) connected by a set of edges (branches). If the graph has polarity or direction, the edges have arrows, and the graph is said to be directed. In this report we are concerned only with directed graphs. Two very simple directed graphs are illustrated in Figure 1.

The ecological graphs utilized herein are based largely on graph theoretical techniques of network analysis, for which the theory has been clearly and concisely presented by Mason and Zimmermann (1960). To analyze a network, each edge connecting two vertices is given a coefficient, a "transfer function" or "branch transmission." The "transmission" from one vertex A to a distant one C can then be expressed as a combination of these individual coefficients. The important principle is that the value of any vertex is the sum of the directed inputs, regardless of the outputs. In the very simple case of Fig-

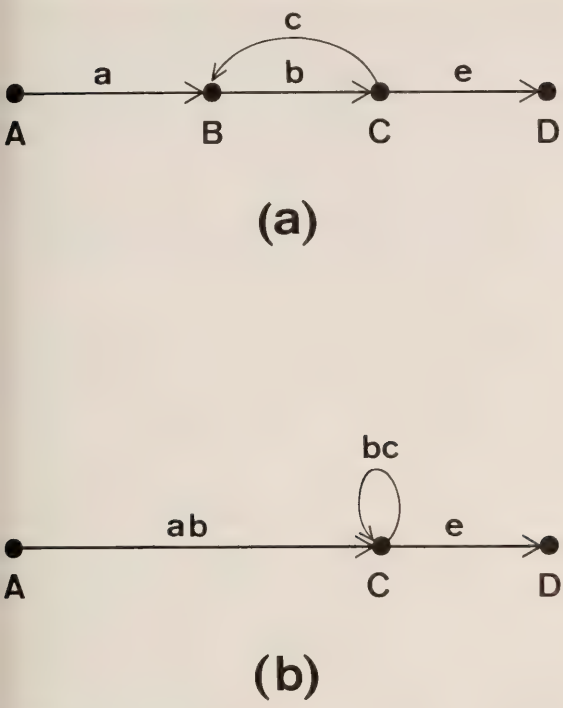


FIGURE 1.—An illustration of two simple directed graphs. A "self-loop" is shown in part (b) of the figure.

ure 1(a), the value of B is equal to the input from A plus the input from C:

$$B = aA + cC. \quad (1)$$

Similarly, the value of C is equal to the only input:

$$C = bB. \quad (2)$$

Substituting B from Equation (1) into Equation (2) and solving for C gives:

$$C = \frac{abA}{1-bc}. \quad (3)$$

Thus the ratio of the value of C to the value of A is:

$$\frac{C}{A} = \frac{ab}{1-bc}, \quad (4)$$

which is the transmission from A to C. This type of term is used later as a biomass ratio or "trophic efficiency."

It can easily be seen that the graph in Figure 1 simply represents a set of linear algebraic equations. Such sets of equations can, of course, be solved classically. However, solution by inspection of some graphs or parts of graphs is possible. For example, in the graph of Figure 1(a), observe that:

$$C = (a \times b) \times A + (c \times b) \times C. \quad (5)$$

The graph can be simplified to that shown in Figure 1(b). A "self-loop" has been created that has the effect of making the value of C to be $\frac{1}{1 - \text{loop transmission coefficient}}$ times what it would have been without the loop. The situation becomes only slightly more complex when the transmission from A to D is considered. The value of D can be obtained from the value of C in Equation (3) as:

$$D = eC = e \cdot \frac{abA}{1-bc}. \quad (6)$$

Or, making use of the known effect of a self-loop, it is possible to simply see by inspection of Figure 1(b) that:

$$D = (abe)A \cdot \frac{1}{1-bc} = e\,\frac{abA}{1-bc} \quad (7)$$

These simple principles and techniques are considered adequate for formulating some useful trophic graphs.

GRAPH OF A TROPHIC UNIT

Graph theory has been applied to the analysis of a variety of problems in engineering, operations research, and the social sciences (Berge, 1958; Busacker and Saaty, 1965; Kaufmann, 1967; Harary, 1969). Its use in biological sciences has been much more limited. However, Benzer (1959) and Maruyama and Yasuda (1970) have applied these concepts to genetics, and Landau (1955) and Trucco (1957) have used graph theory in describing animal behavioral problems. Menshutkin (1969) appears to have been the first to apply graph theory to the study of communities of aquatic organisms. He used graph theory to derive expressions to illustrate the relationship of the biomass of harvested organisms (fish) to primary production under

specific conditions. He graphed the relationship between a prey and a predator as shown in Figure 2(a). For simplicity, all the vertices (capital letters) can be standardized in energy units (or energy per unit time). The lower case coefficients are dimensionless constants or have a dimension of reciprocal time with values between zero and 1.0. Vertices and coefficients are listed in Table 1. Subscript 1 refers to the prey and subscript 2 refers to the predator. When another trophic level is added later, use of these subscripts can be easily extrapolated. For example, D_{12} in Figure 2(a) is the amount of Prey 1 accessible to Predator 2; D_{24} in a later graph is the amount of Prey 2 accessible to Predator 4.

The symbols used in Figure 2 are further defined in the following manner.

TABLE 1.—Description of the vertices and coefficients utilized in model development.

P	= (net) production	
Q	= loss by "respiration"	
q	= "respiration" coefficient	$Q = qB$
B	= biomass	
M	= loss by natural mortality	
m	= natural mortality coefficient	$M = mB$
F	= loss by exploitation (fishing)	
f	= exploitation coefficient	$F = fB$
U	= loss in undigested or unassimilated food	
R	= actual food ration	$U = (1 - k)R$
kR	= food assimilated (gross production)	
k	= digestion or assimilation coefficient	
P	$= kR - Q$	
D_{12}	= accessible food	
d_{12}	= accessibility coefficient	$D_{12} = d_{12}B_1$
H_{12}	= maximum ration (most a predator would ever consume)	
h_{12}	= maximum ration coefficient	$H_{12} = h_{12}B_2$
R_{12}	$= a_{12}H_{12} + b_{12}\delta_{12}$	
δ_{12}	$= D_{12} - H_{12}$	
a_{12}, b_{12}		feeding coefficient

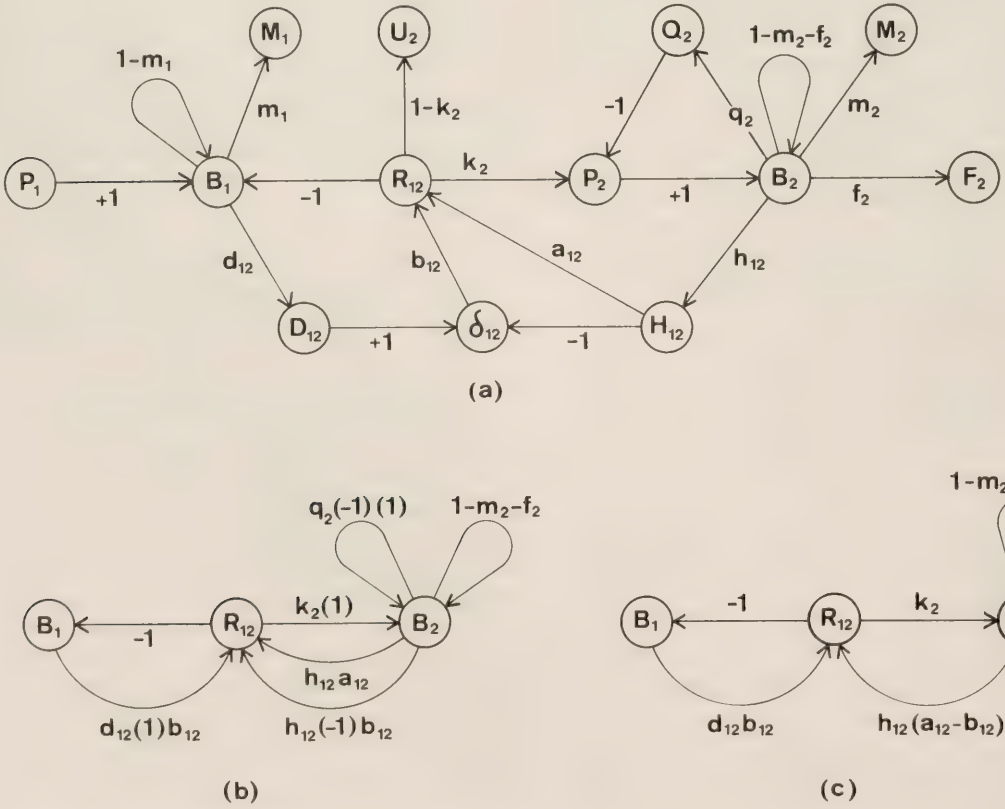


FIGURE 2.—Trophic graphs of Species 2 preying on Species 1. Part (a) illustrates Menshutkin's (1969) original formulation, and parts (b) and (c) represent the successive application of network analysis to obtain the basic trophic unit.

P in the graph is what is usually called net production (an energy rate). Net production P, is equal to gross production, i.e., assimilated food, kR, minus respiration, Q. Summing inputs at the graph vertex P_2, the value of P_2 is:

$$P_2 = k_2R_{12} - Q_2 . \qquad (8)$$

Respiration, Q, is expressed as the product of biomass and a "respiration coefficient," q:

$$Q = qB,$$

where B is the biomass (standing energy crop) of a species.

M is natural mortality, considered proportional to biomass;

$$M_1 = m_1B_1, \qquad M_2 = m_2B_2. \qquad (9)$$

Constancy of these coefficients is assumed.

F is fishing mortality which is used if an exploited population is considered. Death due to any other specific cause can be separately considered in a similar manner.

U is energy in the undigested (unassimilated) portion of food eaten, and k is the "digestion coefficient." The predator assimilates a fraction k of the ration R eaten, and the remaining energy, $U = (1 - k)R$, is lost.

Upon first inspection of the graph, it may be disconcerting to see vertices representing quantities such as biomass (energy) in the graph with vertices representing quantities such as production (energy per unit time). The confusion is resolved by realizing that the graph is not a pure flow network. It merely shows some assumed relationships, and at each vertex the same rules apply. For example, at vertex B_1 in Figure 2(a):

$$B_1 = (+1)P_1 + (-1)R_{12} + (1 - m_1)B_1, \qquad (10)$$

or,

$$P_1 - B_1 + B_1 - m_1B_1 = R_{12}. \qquad (11)$$

Net production — Natural mortality = Remainder eaten by predators.

Thus interpreted, the graph represents the relationships correctly.

An important feature of this formulation is the attempt to approximate the density dependence of feeding rate. Formulations for species interactions such as the classic equations of Lotka and Volterra express rates of change of the number or biomass of a species as products of coefficients and numbers or biomass of the interacting species. This approach has involved the assumption that feeding rate is independent of the abundance of prey and it is an oversimplification which results in an inherently unstable system. The experimental work of Ivlev (1961) provided a density-dependent feeding relation:

$$R = H\,(1 - e^{-\eta p}), \qquad (12)$$

where: H = the "maximum ration" of the predator, the most it would ever eat (or the maximum rate at which it would feed) no matter how much food were available;

R = the "actual ration" of the predator, the amount actually eaten (or the rate at which it feeds) under an actual condition of food availability;

p = the density or biomass of the prey population;

and η = a coefficient.

A linear approximation of this relationship, following Menshutkin (1969), can be used in the graph model. A parameter δ_{12} is defined as:

$$\delta_{12} = D_{12} - H_{12} , \qquad (13)$$

where: D_{12} = the amount of the prey biomass accessible to the predator $D_{12} = d_{12}B_1$. A constant of proportionality to prey biomass is assumed.

H_{12} = as defined above. Since H_{12} is obtained as a fraction of predator biomass ($H_{12} = h_{12}B_2$), the assumption is introduced that all predator individuals feed at the same rate.

The "actual ration" of the predator is then defined as:

$$R_{12} = a_{12}H_{12} + b_{12}\delta_{12} , \qquad (14)$$

where a_{12} and b_{12} are fractional coefficients.

This linear expression is used to approximate the following modification of Ivlev's exponential relation:

$$R = H(1 - e^{\frac{-\xi D}{H}}), \qquad (15)$$

where D and H are defined as before.

The implementation of Equation (14) in the graph of Figure 2(a) is seen by summing inputs at vertex δ_{12}:

$$\delta_{12} = (+1)D_{12} + (-1)H_{12} = D_{12} - H_{12}, \qquad (16)$$

and at vertex R_{12}:

$$R_{12} = a_{12}H_{12} + b_{12}\delta_{12}. \qquad (17)$$

Although lacking in mathematical rigor, this linear approximation can be made to give reasonably accurate results over a limited range of prey density, and it is considered to be an improvement over the simple density-independent assumption. Figure 3 provides a sample comparison of an Ivlev exponential relationship according to Equation (15) with the linear approximation of Equation (14). The coefficients a and b should, of course, be chosen in any real case to approximate either a desired analytic function of known utility or a set of data on feeding observations.

The "network analysis" techniques described previously were applied to the graph of Figure 2(a) to produce the simplified graphs shown as Figure 2(b) and Figure 2(c). The derivations

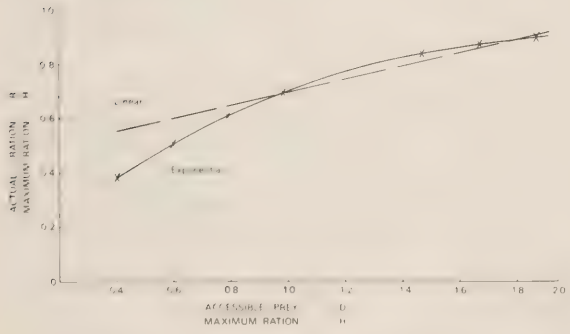


FIGURE 3.—Linear and exponential approximations of feeding behavior.

used do not require P_1 or m_1. Furthermore, M_1, M_2, and U_2 cannot give "inputs" at any vertex since they are all directed outward. Therefore, the above parameters were eliminated with no effect on the solutions. Vertices P_2 and Q_2 were absorbed using graph theory network techniques to produce Figure 2(b). The same figure shows the similar absorption of vertices D_{12}, δ_{12}, and H_{12}. Parallel inputs to a vertex can be combined. In this case, the two self-loops at vertex B_2 were combined, and the two edges from B_2 to R_{12} were combined. The resulting simplified graph, Figure 2(c), is the most basic graph that expresses the assumed relationships.

The above formulation describes a two-species predation model where Species 2 preys on Species 1. At this trophic level, and for the formulations to be used, the term "predation" is applied in its broadest sense. Since the formulation does not make use of production, mortality or any other vital property of Species 1, Species 1 is really just a resource. It could be vegetation, or with some reinterpretation of coefficients, even living space. Clearly, the above graph is a building block from which a variety of more complex food webs can be constructed. Only limited applications of this concept are made in the following material, and its validity awaits the test of further applications.

SOME MODELS AND THEIR INTERPRETATION

Since relatively little observational information is available concerning the important problem of community interactions, it was believed that a model study such as this might assist in a further understanding when additional observational data are taken.

Competitive and predatory interactions, with and without exploitation, were examined using trophic graphs made from the building block developed previously. Figure 4 shows Species 2 and Species 3 competing in their utilization of resource B_1. A relation was derived for the ratio of the biomass of each of the competitors to that of the resource: B_2/B_1 and B_3/B_1. In either case this was done by writing the very simple linear equations for each of two vertices

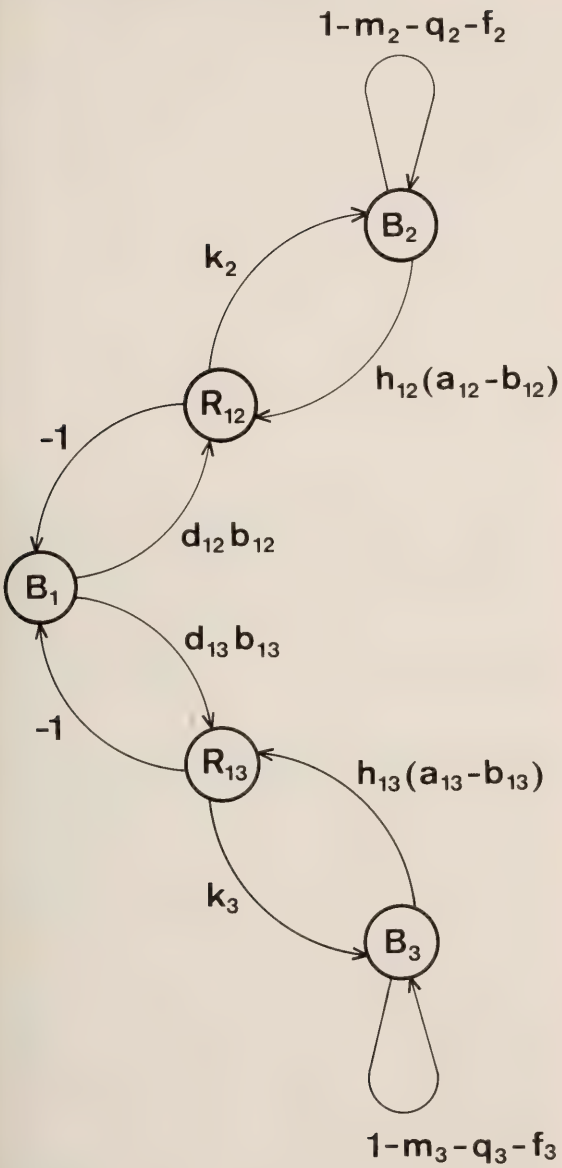


FIGURE 4.—Trophic graph of Species 2 and Species 3 preying on Species 1.

and solving them simultaneously in the classical manner. For competitor Species 2, R_{12} was written as the sum of its inputs in the graph, and B_2 was written as the sum of its own inputs. In this case there are two equations in the three variables B_2, B_1, and R_{12}. R_{12} was eliminated to give B_2/B_1 in terms of coefficients. B_3/B_1 was derived in a similar manner, and division gave the ratio of the biomass of the two competing species B_2/B_3 as follows:

$$\frac{B_2}{B_3} = \frac{k_2 d_{12} b_{12} V}{k_3 d_{13} b_{13} V'} \qquad (18)$$

where: $V = m_3 + q_3 + f_3 - k_3 h_{13}(a_{13} - b_{13})$
$V' = m_2 + q_2 + f_2 - k_2 h_{12}(a_{12} - b_{12})$

Inspection of Equation (18) reveals that if the two species compete exactly equally, or are exploited equally, the ratio is unity. This is entirely the expected result. By giving one species or the other a competitive edge in one or another of the coefficients, it is apparent that the B_2/B_3 ratio can be changed.

The simplest subweb involving predation on two competing species is shown in Figure 5. In this subweb Species 4 preys on Species 2 and Species 3, and Species 2 and Species 3 prey on Species 1. The procedure for deriving the ratios B_2/B_1 and B_3/B_1 was exactly as described above. That is, an equation was written for each

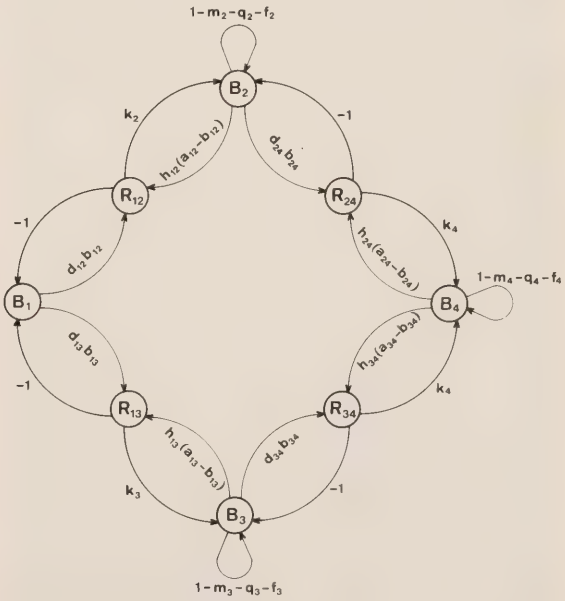


FIGURE 5.—Trophic graph of a 4-species subweb. In this case Species 4 preys on Species 2 and Species 3, and Species 2 and Species 3 prey on Species 1.

vertex except B_1, and the equations were solved simultaneously. In this case there are seven equations, and the work of classical solution was not excessive. The result was found to be:

$$\frac{B_2}{B_3} = \frac{W - k_2 d_{12} b_{12}(XY + Z)}{W' - k_3 d_{13} b_{13}(XY' + Z')} \qquad (19)$$

where:

$$W = k_3 k_4 d_{13} b_{13} d_{34} b_{34} h_{24}(a_{24} - b_{24})$$
$$W' = k_2 k_4 d_{12} b_{12} d_{24} b_{24} h_{34}(a_{34} - b_{34})$$
$$X = k_4 h_{24}(a_{24} - b_{24}) + k_4 h_{34}(a_{34} - b_{34}) - m_4 - q_4 - f_4$$
$$Y = k_3 h_{13}(a_{13} - b_{13}) - d_{34} b_{34} - m_3 - q_3 - f_3$$
$$Y' = k_2 h_{12}(a_{12} - b_{12}) - d_{24} b_{24} - m_2 - q_2 - f_2$$
$$Z = k_4 d_{34} b_{34} h_{34}(a_{34} - b_{34})$$
$$Z' = k_4 d_{24} b_{24} h_{24}(a_{24} - b_{24})$$

Questions of interest here were the effects on biomass ratios of the competitors as a function of various competitive coefficients and exploitation, and the difference in these effects with and without predation on the competitors. "Coefficient" values from Menshutkin (1969) were introduced for the coefficients for predation by Species 4 on Species 2 and Species 3 (the same coefficients for both—equal predation). Basically the same coefficients were used for the competition of Species 2 and Species 3 as well. Coefficients were held constant except for the one whose effect was being considered. Using such values, the equations were simplified, and in most cases Species 3 was then given the nominal value of the competitive variable of interest while the value of that variable for Species 2 was made to vary above and below the nominal. This range of variation of Species 2 was expressed as the ratio coefficient 2/coefficient 3. The same process was performed for the earlier formulation without predation (Equation 18). Thus ratios B_2/B_3 were obtained from both cases—with and without predation.

A brief examination was made of the effect of various exploitation strategies on the relative stability of two model ecosystems, one with predation and one without predation. These systems are described by Equations (18) and (19), and stability was measured by the change in biomass. Figure 6 illustrates the results of various types of exploitation on the two systems. It is

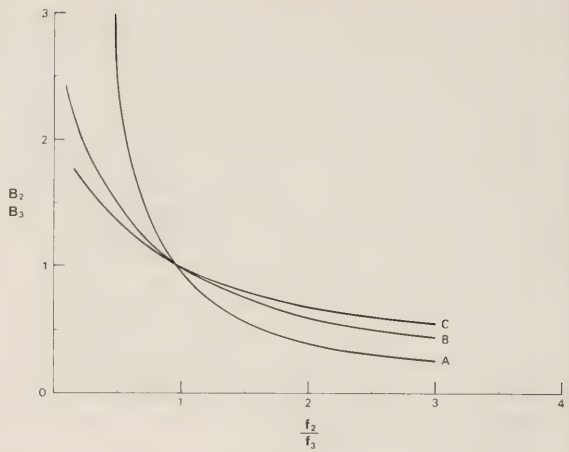


FIGURE 6.—Effects of predation and exploitation on model ecosystem stability as measured by biomass ratios. Curve A illustrates a 4-species subweb in which there is no exploitation of the top predator. Curve B illustrates a 3-species subweb with no top predator. Curve C illustrates a 4-species subweb with exploitation of the top predator as well as prey species 2 and 3. All numerical values of coefficients are from Menshutkin (1969). The nominal value of f_3 was taken as 0.3.

apparent from an examination of this figure that the most stable conditions examined involved predation as well as exploitation of the predator and the prey species. However, the system involving no top predator seemed to be more stable under exploitation of both prey species than the system involving predation, but with no exploitation of the top predator.

For different types of competitive advantage of one species over the other, the effect of predation on biomass ratios may be very different. Figure 7 demonstrates the effect of unequal competition in the coefficient d, which relates to the availability of the resource to Species 2 and Species 3. Without predation, the ratio B_2/B_3 of biomasses of the competitors is always the same as their d ratio. With predation, the ratio takes the much different form indicated. The values used for the d_{12}/d_{13} ratio ranged from 2.7 to 0.37. This range of values produces a full range of B_2/B_3 ratios, from the point where Species 3 becomes extinct, to the point where Species 2 becomes extinct. For the coefficient d, the results are not dependent upon the absolute value of d.

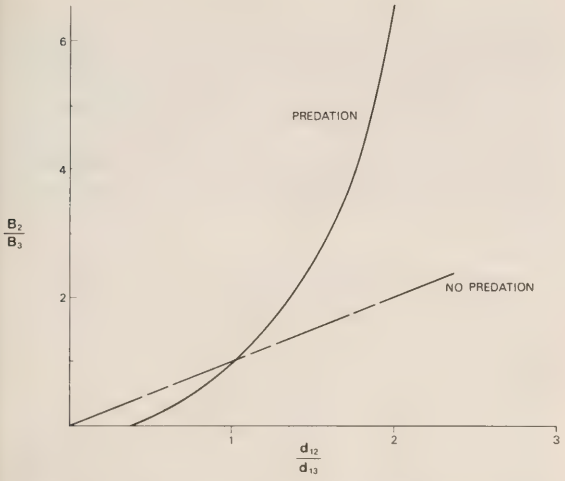
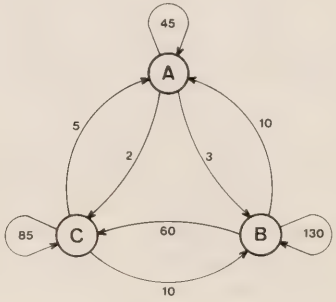


FIGURE 7.—An illustration of the effect of predation (as measured by biomass ratios) on competition as measured by changes in the ratio of the resource accessibility coefficient d for the two species.

The results shown in Figure 7 clearly indicate that some of the competitive coefficients have a very large influence on the relative stability of interacting systems. They suggest that if the stress of exploitation or other environmental stresses interact with other model coefficients as, for example, in a simple predator-prey interaction, the system may respond very violently, with the rapid extinction of one or the other of the competing species.

In some instances it may be desirable to have some rough empirical measure of the stability of exploited ecosystems consisting of interacting species. As Margalef (1969) has indicated, an adequate measure of community stability must include a measure of diversity as well as a measure of persistence. Furthermore, Margalef attempted to formulate a generalized mathematical model for their interdependence. It is suggested that an additional application of graph theory may also be utilized to provide some empirical indication of stability and persistence of communities subjected to either environmental or exploitive stresses, assuming certain types of background information are available.

Consider the following hypothetical example. Three communities of fishes (A, B, C) are subjected to various levels of exploitation. Assume that some crude index of diversity or community structure has been established which permits identification of the three communities as mutually exclusive groups. Assume that the three communities are sampled again during the course of a year, and that the frequency of samples which resemble the previously defined community as well as the frequency of samples which resemble the other two communities are listed. These frequencies can be displayed in the form of a network as shown in Figure 8. The data



$$F_0 = \begin{bmatrix} 45 & 3 & 2 & 50 \\ 10 & 130 & 60 & 200 \\ 5 & 10 & 85 & 100 \end{bmatrix} \qquad M = \begin{bmatrix} .90 & .06 & .04 \\ .05 & .65 & .30 \\ .05 & .10 & .85 \end{bmatrix}$$

$$M^2 = \begin{bmatrix} .8150 & .0970 & .0880 \\ .0925 & .4555 & .4520 \\ .0925 & .1530 & .7545 \end{bmatrix} \qquad P_0 = \begin{bmatrix} 50 & 200 & 100 \end{bmatrix}$$

$$P_0 M^2 = \begin{bmatrix} 50 & 200 & 100 \end{bmatrix} \begin{bmatrix} .8150 & .0970 & .0880 \\ .0925 & .4555 & .4520 \\ .0925 & .1530 & .7545 \end{bmatrix} = \begin{bmatrix} 68.50 & 111.25 & 170.25 \end{bmatrix}$$

FIGURE 8.—Example of a hypothetical network showing the frequencies of samples resembling their initial structure as well as those of the other two community structures. In this example F_0 is the matrix of frequencies at the end of the first sampling period, M is the corresponding probability matrix, M^2 is the square of the probability matrix and P_0 is the vector of frequencies by community type. P_0M^2 is the matrix-vector product expressing the expected new frequencies by community type at the end of the second sampling period under the assumption that the probability matrix remains constant during the time interval.

from the network is presented as a matrix (F_o of Figure 8) of frequencies which was normalized to form a probability matrix (M of Figure 8). This probability matrix M is one in which the i, j entry gives the proportion of the samples from community v_i which resembled community v_j during the sampling period. An important theorem concerning probability matrices states that if B and C are probability matrices, so is their product BC. A corollary to this theorem states that if M is a probability matrix, then so is every power M^n, for any positive integer n. If the assumption is made that the probability matrix M remains constant over time, then if one knows the initial frequency matrix F_o and the probability matrix M, it is possible to find the sample frequency distribution at a subsequent time t_n by finding the nth power of M and then forming the product P_oM^n where P_o is the vector of row sums equal to the initial vector of frequencies by community type. In our case the frequency in year 2 is $F_2 = P_oM^2$. This matrix-vector multiplication is illustrated in the lower part of Figure 8. It is suggested that this derived frequency might be useful as the expected value basis for comparison with the sample observations made during subsequent years, if it is assumed the probability matrix remains constant over time.

CONCLUSIONS

The examples provided in this study are given primarily to illustrate the wide range of possibilities for the use of graph theory in studying the stability of interacting competitive and predatory relationships. The tentative results of this model study suggest that a nonselective exploitation strategy, which includes both predator and prey organisms, may be "best" from the point of view of maintaining community stability in complex ecosystems. The high desirability of obtaining experimental values for certain coefficients was also pointed out.

The limitations of a linear, steady-state model are many and obvious. However, if such a model can sometimes be utilized to provide approximate results suitable for use in practical management at the early stages of marine ecosystem management, then the model is a worthwhile tool, and the method utilized has some merit. If the method (graph theory) can be used not only to obtain some basic insight into system behavior but can also be used as an empirical tool, then it seems particularly worthwhile. Both these possibilities seem to await the results of future imaginative development.

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NITROGEN EXCRETION BY ANCHOVY (*ENGRAULIS MORDAX* AND *E. RINGENS*) AND JACK MACKEREL (*TRACHURUS SYMMETRICUS*)[1]

JAMES J. McCARTHY[2] AND TERRY E. WHITLEDGE[3]

ABSTRACT

Teleost fish have been shown to excrete a variety of nitrogenous substances among which are ammonia, urea, and creatine. Previous reports show values for excretion of nearshore or bottom fish but not of pelagic species.

Two species of anchovy and jack mackerel were placed in chambers and their nitrogenous excretion products were measured. Ammonia, urea, and creatine accounted for 82% of the total nitrogen excreted by *Engraulis mordax* and the identified fraction was 83% ammonia, 16% urea, and 1% creatine.

The significance of pelagic fish as a source of ammonia and urea in California coastal waters is discussed.

On the basis of the major end product of their protein catabolism, animals are classified as ammonotelic, ureotelic, and uricotelic. Although these categories can be useful in evolutionary considerations (Baldwin, 1964), they are somewhat arbitrary in that the excreta of most animals contain a mixture of ammonia, urea, and uric acid. Mammals, elasmobranch fish, some amphibians, and some reptiles are considered to be ureotelic; teleost fish, some amphibians, and most invertebrates are ammonotelic; and birds and some reptiles are uricotelic (Baldwin, 1964). In ureotelic animals urea is produced via the ornithine cycle. It is, however, unlikely that this metabolic pathway is operative in nonureotelic organisms such as some teleosts, which excrete substantial quantities of urea. Brown and Cohen (1960) have shown that no marine teleost has the enzymes necessary for the first two steps in the ornithine cycle. The complete complement of ornithine enzymes has been found in the coelacanth however (Brown and Brown, 1967).

Arginase is present in the livers of teleost fish and hence dietary arginine has been suggested as a source of urea (Hunter and Dauphinee, 1924-1925; Hunter, 1929), but this suggestion is considered unlikely since arginine is an essential amino acid for this group of organisms (Forster and Goldstein, 1969). Purine catabolism also has been suggested as a means of urea formation via uricolysis (Brunel, 1937), and in support of this Goldstein and Forster (1965) found uricolytic activity in the livers of five species of marine and freshwater teleosts.

Delaunay (1929), Grafflin and Gould (1936), Grollman (1929), and Smith (1929) determined the composition of the urine of eight species of marine teleosts and their results were summarized by Scheer and Ramimurthi (1968). The proportions of various components of the total nonprotein urinary nitrogen varied greatly within, as well as between, species (ammonia varied from 0.5 to 9.6%, urea varied from 0.1 to 30.8%, creatine varied from 6.5 to 61.7%, and amino-N varied from 4.0 to 21.4%). In 1929 Smith used a divided chamber to permit separate determinations of the nitrogen released by the gills and by the kidneys, and his results showed that essentially all of the ammonia and urea released originated from the gills. In addition to these compounds, the branchial excreta consisted of amine or amine oxide derivatives while the less diffusible nitrogenous end products such as creatine, creatinine, and uric acid were excreted solely by the kidneys. It is therefore

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apparent that a release rate with ecological significance would have to consider both branchial and renal release.

Since the only data available from which one can calculate nitrogenous release rates for marine teleosts are for nearshore or bottom fish such as the sculpin, the starry flounder, and the blue sea perch (Wood, 1958), the following work was undertaken using significant pelagic species in order to assess the importance of marine teleosts as a source of ammonia, urea, and creatine in the euphotic zone.

METHODS

Experiments with the northern anchovy, *Engraulis mordax*, were conducted in August 1970, in the laboratories of the Fishery-Oceanography Center, La Jolla, California. Between experiments the fish were kept in a tank of flowing seawater and, unless specified otherwise, were fed frozen brine shrimp daily. For each experiment ten fish were placed in a 32-liter circular Plexiglas chamber similar to that described by Lasker (1970). During the first experiment the chamber was darkened and 24°C seawater flowed through it at a constant and determined rate. Beginning at the time the fish were introduced, effluent was sampled at 10-min intervals for 40 min. The fish had not been fed for 24 hr. For experiments 2 and 3 the flowing system was not used. The chamber was filled initially with seawater and during the experiments was exposed to room light. The temperature during experiment 2 was 24°C and water samples were taken at 10-min intervals for 40 min. The fish had been fed 30 min prior to their placement in the chamber. The temperature during experiment 3 was 21.5°C and water samples were taken at 10-min intervals for 70 min. The fish had not been fed for 48 hr and just after the 30-min sampling, 2.49 g of frozen brine shrimp were thawed and added to the chamber (the first and second portions of experiment 3 will be referred to as 3a and 3b). An appropriate control was run to determine the effect of the brine shrimp on the ammonia, urea, creatine, and total nitrogen concentrations.

Ten fish from the group used for experiments 1 and 2 and the ten used for experiment 3 were sacrificed for weight determinations. Wet weight determinations were made after blotting the specimens on filter paper, and dry weight was determined after they had been dried at 60°C for 96 hr.

Experiments with the Peruvian anchovy, *Engraulis ringens*, were conducted off the coast of Peru in April 1969, during the RV *Thompson* cruise 36. The methods of collection were described by Whitledge and Packard (1971). Release rates for urea and ammonia were determined for each of three fish in separate one-liter volumes of 0.45μ m Millipore^R filtered seawater at 15°C. Each experiment was run until the animal died (approximately 90 min).

Experiments with the jack mackerel, *Trachurus symmetricus*, were conducted off the coast of California in July 1970, during a cruise of the RV *Alpha Helix* for the Institute of Marine Resources Food Chain Research Group. Of three specimens caught with lure and line, two were placed in a 42-liter Plexiglas deck tank which was continually flushed with surface seawater, and the third, which had been injured when caught, was sacrificed for a weight determination. After approximately 5 hr the fish were transferred to a similar tank recently cleaned and filled with 19°C surface seawater which had been filtered through a 173 μm nylon mesh. Samples for ammonia and urea analyses were taken at the beginning and at the conclusion of the experiment 2 hr later. The fish were kept another 20 hr and released.

For samples from the *E. ringens* experiments ammonia was determined by a modified form of Johnston's (1966) rubazoic acid method and urea by a urease hydrolysis coupled with the rubazoic acid method. In all other experiments ammonia was determined by the phenolhypochlorite method (Solórzano, 1969) and urea by the urease method (McCarthy, 1970). All determinations were made in duplicate immediately after each experiment. Creatine concentrations were measured using a fluorescent complex with alkaline ninhydrin (Whitledge and Dugdale, in press). Total nitrogen was determined with the ultraviolet oxidation technique

of Armstrong, Williams, and Strickland (1966) as described by Strickland and Parsons (1968), but modified by the addition of sodium hypochlorite (chlorine bleach, 5.25% active ingredients). One ml sodium hypochlorite per 100 ml sample was found to increase the percentage of conversion of creatine to nitrate. If added in excess, the sodium hypochlorite will react with the hydrogen peroxide to release oxygen. The conversion of a standard solution of creatine to nitrate in the digester was 43.4%, but the addition of sodium hypochlorite increased this value to 95.0%. Urea standards showed 96-100% conversion without addition of sodium hypochlorite.

All chambers were washed with either fresh or distilled water immediately prior to each experiment and experimental periods were kept to a minimum in an effort to reduce possible effects of bacteria. Antibiotics interfere with both of the ammonia methods mentioned above, and could not be used to reduce bacterial activity. Wood (1958) showed that in fish excretion experiments running as long as 24 hr, bacteria on the surface of the fish do not affect the results and the concentrations of released nitrogen compounds were unchanged for an additional 24 hr.

The data were analyzed statistically using the Mann Whitney U and the Tukey-Siegel tests to compare the medians and variabilities respectively. Significant differences between experiments were at the 0.05 level.

RESULTS

The release rates for ammonia, urea, creatine, total nitrogen and the ammonia-urea ratios for all experiments are given in Table 1. The results of the *E. mordax* experiments represent the mean of the 10-min interval samples for each experiment. An example of the data obtained in one of these experiments is shown in Figure 1. At the conclusion of the first *E. mordax* experiment all of the fish had acquired darkened dorsal coloration and one was locked into the panic response described below for *E. ringens*. Immediately after release into the large holding tank, food was added and all except the one panicked fish, which died a few hours later, fed normally and regained normal coloration. During the other experiments with *E. mordax*, the fish behaved normally and retained their normal coloration. The fish in the *E. mordax* experiment 3b were restricted from feeding in their normal frenzied manner because of the size of the chamber and at the conclusion a small portion of the food remained uneaten. Creatine and total nitrogen values for the second *E. mordax* experiment indicate that

TABLE 1.—Excretion of nitrogenous compounds by *Engraulis mordax*, *E. ringens*, and *Trachurus symmetricus*.

Species		μg at N/mg dry wt/day				
		Ammonia	Urea	Creatine	Total nitrogen	Ammonia-N / Urea-N
Engraulis mordax						
starved one day	(1)	0.074	0.020			3.70
fed before experiment	(2)	0.185	0.036	0.003	0.273	5.14
starved 2 days	(3a)	0.055	0.021	0.002		2.62
feeding	(3b)	0.076	0.023	0.003		3.45
Engraulis ringens	(1)	0.240	0.083	0.118	0.507	2.90
	(2)	0.281	0.089	0.111	0.700	3.16
	(3)	0.171	0.057	0.104	0.346	3.00
Trachurus symmetricus		0.090	0.017			5.29

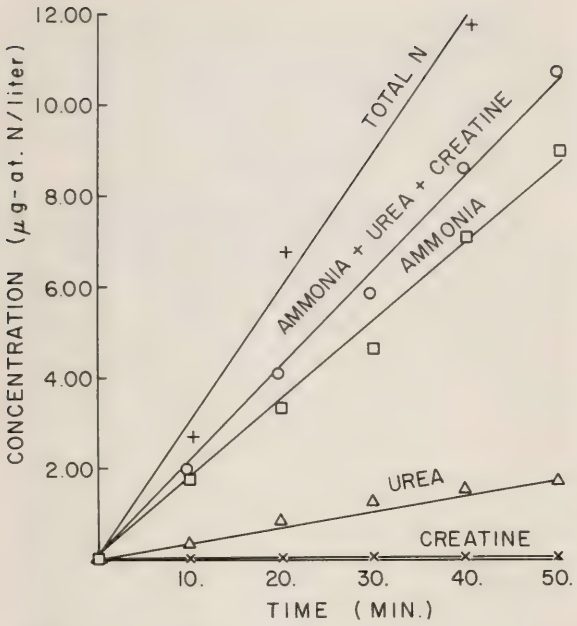

FIGURE 1.—Nitrogen excretion by 10 specimens of *Engraulis mordax* in experiment 2. Specimens were fed 30 min before experiment.

ammonia, urea, and creatine accounted for approximately 82.7, 16.0, and 1.3%, respectively, of the sum of the ammonia, urea, and creatine values. This sum was approximately 82% of the total nitrogen released. The fish used in the *E. mordax* experiments 1 and 2 had a mean wet weight of 13.9 g and a mean dry weight of 3.9 g per animal; those used in the third experiment had mean wet and dry weights, respectivly, of 15.2 g and 4.3 g per animal.

In the *E. ringens* experiments, the sum of the individually measured nitrogen compounds accounted for 69 to 96% of total nitrogen excreted. Relative amounts of ammonia, urea, and creatine averaged 44.6, 14.5, and 21.4%, respectively, while 19.5% was unidentified. Although the specimens of *E. ringens* appeared in good health for the first few hours after capture, their condition deteriorated rapidly after the experiment began. One lived for 83 min, another for 85 min, and the third for 105 min. The behavior pattern was a panic response in which the animals tried repeatedly to swim downward into the bottom of the container and eventually did considerable damage to their heads, resulting in broken blood vessels in their eyes and nasal regions. The dorsal coloration changed from a greenish-grey to jet black during the deterioration, and once an animal locked into this behavior pattern there was apparently no way to reverse it and death was inevitable. The mean wet weight and dry weight per fish for these experiments was 7.0 and 1.9 g, respectively, and nitrogen was found to be 10.9% of dry weight.

The results for the *T. symmetricus* represent a single value for both fish in the same chamber. Prior to, during, and in the 20 hr after the experiment the fish swam about the chamber in a calm manner. The wet weight of the sacrificed fish was 190.0 g.

DISCUSSION

The fish in the *E. mordax* experiment 2 were the most recently fed, and Figure 1 shows that urea, ammonia, and creatine were released at approximately constant rates over the experimental period. Table 1 shows that these release rates for ammonia, urea, and the ammonia-urea ratio were the highest of all the *E. mordax* experiments. The urea release rates for the other experiments (1, 3a, and 3b) were all similar, but the ammonia release rates and the ammonia-urea ratios appear to be related to the length of the starvation period.

For the *E. mordax* experiments, the statistical tests indicated that the ammonia release rates in experiments 1 and 3a and in experiments 1 and 3b were not significantly different within each pair with respect to central tendency. On the other hand there were significant differences between the pairs of ammonia release rates in experiments 1 and 2, 2 and 3a, and 2 and 3b. The variabilities for ammonia release rates for all of the experiments were similar. With regard to the urea release rates, only those for experiments 1 and 2 were significantly different with respect to location of central tendency and none of the experiments differed from each other with respect to variability.

These statistics imply that the effect of feeding is rapidly apparent in the ammonia release rates while it appears more slowly and to a lesser de-

gree in the urea release rates; this is clearly reflected in the ammonia-urea ratios. When the period of starvation was the greatest (experiment 3a) the ratio was the lowest, and when the starvation was least the ratio was the greatest. The ratio for experiment 3b presumably would have increased to a value comparable to that for experiment 2 when the time since feeding had become equal for both.

Upon thawing, the brine shrimp which were used to feed *E. mordax* liberated ammonia, urea, and creatine. If these substances were retained in large quantities by the shrimp, the results of experiments 2 and 3b could have been affected. Such interference is, however, unlikely since only the ammonia release rate increased with feeding in experiment 3. If this increased rate of release had resulted from ammonia liberated from the shrimp after ingestion by the fish, a comparable increase in the rate of urea release would have been expected since the quantities of urea liberated by the shrimp were approximately equal to those of ammonia.

It is important to note that since experiment 3 was conducted at a temperature 2.5°C lower than the other experiments, a correction of the measured rates should be made in order to compare them properly. Since an appropriate Q_{10} value was not available, the correction was not made. Presumably, however, a Q_{10} for an ammonia release rate would be similar if not identical to that for urea, and the ammonia-urea ratio would not be changed with a temperature correction. The lack of both a temperature correction and an appropriate relationship between body size and nitrogen excretion also makes the comparison of data between different species difficult.

The *E. ringens* experiments produced the highest release rates (particularly for creatine) and the lowest ammonia-urea ratios. This can probably be attributed to the high level of activity and/or the poor health of the specimens.

Wood (1958) ran experiments for 24 hr at 12°C, and from his Table 2 and an approximation of 28% wet weight = dry weight, one can calculate ammonia and urea release rates. These calculated mean release rates are 0.0141, 0.0179, and 0.0065 μg at ammonia-N + urea-N/mg dry weight/day, for the sculpin (*Leptocottus armatus*), the starry flounder (*Platichthys stellatus*), and the blue sea perch (*Taeniotoca lateralis*) respectively. These rates are nearly an order of magnitude lower than those reported here, but a temperature correction (assuming a Q_{10} of 2) would bring them within approximately a factor of five. The calculated ammonia-urea ratios for the sculpin, the starry flounder, and the blue sea perch are 3.09, 7.13, and 1.26 respectively. Since the fish used in Wood's studies were nearly ten times larger than the anchovies, were maintained for some time prior to the experiments on a diet of lingcod muscle, and for the experiments were enclosed in chambers barely larger than the fish, it is difficult to compare the results of the different sets of data.

Ammonia and urea are important plant nutrients and it is of interest to examine the significance of fish excretion as a source of these substances in the sea. Whitledge and Packard (1971) estimated that nitrogen excretion by the herbivorous *E. ringens* in the near surface waters of the Peru Current is an order of magnitude greater per unit volume of water than zooplankton excretion and they suggested, on the basis of these rates and measured rates of nitrogen uptake by phytoplankton, that fish excretion may be a major source of the ammonia utilized by phytoplankton in this area.

Off the coast of southern California the contribution of the fish community in the regeneration of ammonia and urea can also be estimated. Integrated values of phytoplankton nitrogen utilization at three stations in the euphotic zone off the coast of San Diego (Stations 1, 4, and 6, McCarthy[4] averaged 0.073 μg at ammonia-N/liter/day and 0.066 μg at urea-N/liter/day. For the area included in the California Cooperative Oceanic Fisheries Investigations (CalCOFI) survey, the total biomass of the most common species of near-surface fish [northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*), jack mackerel (*Trachurus symmetricus*), Pacific saury (*Cololabis saira*), and al-

[4] McCarthy, J. J. The uptake of urea by natural populations of marine phytoplankton. Manuscript in preparation.

bacore (*Thunnus alalunga*)] is estimated at 20-25 $\times$ 10^6 metric tons wet weight (Dr. P. E. Smith, personal communication). Using an area of 70 $\times$ 10^{10} m^2, a depth of 140 m, an average excretion rate from Table 1 (*E. mordax*, experiments 1 and 2, and *T. symmetricus*), and a conversion factor (dry wt = 28% wet wt) approximate production rates of 0.0075 μg at ammonia-N/liter/day and 0.0015 μg at urea-N/liter/day can be calculated. These rates would account for 10% of the ammonia and 2% of the urea utilized by the phytoplankton.

Other investigators—Harris, 1959; Dugdale and Goering, 1967 and 1970; and Martin, 1968—have attempted to balance ammonia utilization by phytoplankton and excretion by zooplankton in Long Island Sound, the Bermuda region, the Peru Current and Narragansett Bay respectively. Further calculations can be made for the area off southern California to compare the significance of fish ammonia and urea excretion to that of zooplankton. A zooplankton standing crop estimate of 0.125 mg dry wt/liter was calculated from 10 years of data collected in the California Current as part of the CalCOFI program by multiplying the mean catch by a factor of 3 to compensate for the biomass of the smaller zooplankton lost through the 0.505 mm mesh (Dr. P. E. Smith, personal communication). Using average excretion rates for recently fed zooplankton (*Calanus helgolandicus*, *Calanus chilenis*, and *Clausocalanus* sp.) of 0.73 μg at ammonia-N/mg dry wt/day and 0.36 μg at urea-N/mg dry wt/day (McCarthy, 1971) average regeneration rates of 0.090 μg at ammonia/liter/day and 0.045 μg at urea-N/liter/day can be calculated. These rates would account for 123% of the ammonia and 68% of the urea utilized per day. If on the other hand, microzooplankton and zooplankton biomass data collected from April through September 1967 in the same approximate area as two of the three stations used for the phytoplankton utilization calculations are applied (Beers and Stewart, 1970; Mullin and Brooks, 1970) the calculated regeneration would be 0.020 μg at ammonia-N/liter/day and 0.010 μg at urea-N/liter/day. These rates account for 27% of the ammonia and 15% of the urea utilized by the phytoplankton. Hence, the fish contribution would amount to 8-27% of the ammonia and 3-13% of the urea released by both groups of organisms. There undoubtedly are, however, situations in which large fish or schools of fish (the mean density of an *E. mordax* school is estimated as the equivalent of 1,300 10-cm fish/m^3, Dr. P. E. Smith, personal communication) are more important than zooplankton in supplying ammonia and urea to a particular parcel of water.

Obviously these calculations are based on many simplified assumptions. Other than the fact that the zooplankton and fish biomass estimates are averages for larger areas and longer periods of time than can be represented by the phytoplankton utilization rates, perhaps the most poorly based assumption is the application of mean excretion rates for three zooplankton species and two fish species to the entire zooplankton and fish populations. More reliable estimates of excretion rates are needed for smaller species of zooplankton and larger species of fish.

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ELECTROPHORETIC INVESTIGATION OF THE FAMILY SCORPAENIDAE

ALLYN G. JOHNSON, FRED M. UTTER, AND HAROLD O. HODGINS[1]

ABSTRACT

Thirty-one species of three genera of the family Scorpaenidae were separated into 17 groups based on starch gel electrophoretic comparison of muscle proteins and six enzymatic systems. This study concluded that relatively greater similarity existed between the Pacific *Sebastes* and the Atlantic *Sebastes* than between either and the other genera. Ten of the 27 species of Pacific *Sebastes* tested had unique biochemical profiles which may be useful for identification of specimens.

The family Scorpaenidae contains several genera in the Pacific and Atlantic Oceans. On the Pacific coast of North America there are four genera—*Sebastes*,[2] *Sebastolobus*, *Scorpaena*, and *Scorpaenodes*. *The genus of Pacific Sebastes* contains over 50 species (Tsuyuki et al., 1968). In this genus new species and extensions of known distribution ranges have been described in recent years (Westrheim, 1965; Westrheim and Tsuyuki, 1967; Nishimoto, 1970; Tsuyuki and Westrheim, 1970). At present there are difficulties in showing taxonomic relations and, in some instances, in making positive identification of specimens using morphometric and meristic methods, although taxonomic relations can be obtained by biochemical methods. Starch gel electrophoresis—developed by Smithies (1955)—coupled with histochemical procedures (Hunter and Markert, 1957) is one of the best biochemical techniques for taxonomic studies.

Scorpaenid muscle proteins and hemoglobin were investigated by starch gel electrophoresis by Tsuyuki et al. (1968). They suggested that the electrophoretic evidence did not support the separation of the two genera *Sebastodes* and *Sebastes*. Chu (1968), using disk electrophoresis of muscle proteins, found different patterns in two out of eight species of *Sebastodes*. Altukhov and Nefyodov (1968) demonstrated serum protein differences between *Sebastes marinus* and *S. mentella* using agar gel electrophoresis.

This paper reports the findings of our investigation of proteins and six enzyme systems found in the skeletal muscle or liver of members of the family Scorpaenidae. Our study involved 27 species of Pacific *Sebastes*, 2 of the Atlantic *Sebastes*, and 1 each of *Sebastolobus* and *Helicolenus*. We present information on the relative biochemical similarity between genera and a key which separates 10 of the 27 Pacific *Sebastes* species studied. This was not a genetic study per se but a research which demonstrated repeatable biochemical differences between species. The observed constancy of biochemical characters examined within a species in samples taken at different ages, depths, and geographic locations is evidence that the reported differences between species are, indeed, genetic. Alternate explanations for such repeatable expression of proteins under the above conditions seem much less likely.

MATERIAL AND METHODS

Sampling data including location, species, and number of individuals collected are given in Table 1.

Most samples were frozen quickly after capture, but in some instances were kept on ice for short periods; all samples were kept frozen at —20°C after receipt at the laboratory until tested. Extracts were prepared by mixing equal

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[2] In this paper we follow the designation of Bailey (1970) and Chen (1971), considering *Sebastodes* as *Sebastes*. Members of the genus *Sebastes* that were collected along the Pacific Coast of North America are signified in this paper as Pacific *Sebastes*.

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TABLE 1.—Location and number of specimens of Scorpaenidae collected, 1968-70.

Species	Location[1]						Total number of fish
	A	B	C	D	E	F	
Pacific *Sebastes*							
S. aleutianus	10	--	6	--	--	--	16
S. alutus	217	--	843	--	--	--	1,060
S. auriculatus	--	76	--	--	--	--	76
S. aurora	3	--	--	--	--	--	3
S. brevispinis	5	--	40	--	--	--	45
S. caenaematicus	--	--	--	--	--	3	3
S. caurinus	--	283	--	--	--	--	283
S. chlorostictus	--	--	--	--	1	--	1
S. crameri	2	--	16	--	--	--	18
S. diploproa	14	--	--	--	--	--	14
S. elongatus	--	297	96	--	--	--	393
S. entomelas	2	--	2	--	--	--	4
S. flavidus	8	--	--	--	--	--	8
S. helvomaculatus	5	--	19	--	--	--	24
S. levis	--	--	--	--	1	--	1
S. maliger	--	25	--	--	--	--	25
S. melanops	--	28	--	--	--	--	28
S. paucispinis	2	--	15	--	1	--	18
S. pinniger	--	--	24	--	--	--	24
S. proriger	9	--	100	--	--	--	109
S. reedi	1	--	110	--	--	--	111
S. ruberrimus	5	27	5	--	--	--	37
S. rubivinctus	5	--	34	--	--	--	39
S. saxicola	5	--	--	--	1	--	6
S. wilsoni	--	--	1	--	--	--	1
S. variegatus	--	--	--	--	--	1	1
S. zacentrus	1	--	37	--	--	--	38
Atlantic *Sebastes*							
S. marinus	--	--	--	9	--	--	9
S. viviparous	--	--	--	10	--	--	10
Sebastolobus alascanus	--	--	100	--	--	--	100
Helicolenus dactylopterus	--	--	--	10	--	--	10

[1] A = Pacific Coast of Washington and Oregon, 1968-70; B = Puget Sound, Wash., 1968-70; C = Queen Charlotte Sound, B.C., Canada, June 1970; D = West Coast of Britain and Ireland, August 1970; E = Avila Beach, Calif., October 1970; F = Cape Ommaney, Alaska, April 1970.

volumes of tissue and phosphate-buffered physiological saline solution (pH 7.4) into uniform pastes with glass rods. The extracts were tested by electrophoresis without further treatment by (1) drawing them into ¼-inch × 3/16-inch filter paper inserts (Schleicher and Schuell grade S and S No. 470)[3], placed on the surface of the tissue-saline mixture, and (2) placing the inserts into starch gels.

Electrophoresis in starch gel followed the methods of Kristjansson (1963). All but two of the biochemical systems were resolved well using a buffer system described by Markert and Faulhaber (1965). Lactate dehydrogenase and phosphoglucomutase were best resolved by using the buffer system described by Ridgway, Sherburne, and Lewis (1970). Gels consisted of 35 g starch plus 250 ml of buffer. A voltage of 300 was applied for 10 min; sample inserts were removed and 400 v applied until indicator dye markers reached a point 6 to 9 cm anodal to the origin. The gels were cooled during electrophoresis by placing ice packs on glass plates on top of the gels. After electrophoresis, bands reflecting enzyme activity were detected by the following methods:

Tetrazolium oxidase (TO) (after Brewer, 1967, and Johnson, Utter, and Hodgins, 1970b):
- 5 mg phenazine methosulfate (PMS)
- 3 mg p-nitro blue tetrazolium (NBT)
- 40 ml tris-citrate buffer (0.03 M tris, 0.005 M citric acid, pH7.0)

L-alpha-glycerophosphate dehydrogenase (αGPDH) (after Nyman, 1967, and Johnson, Utter, and Hodgins, 1970a):
- 5 mg PMS
- 3 mg NBT
- 5 mg NAD+
- 100 mg L-alpha-glycerophosphate
- 40 ml tris-citrate buffer

Lactate dehydrogenase (LDH):
- 10 mg PMS
- 5 mg NBT
- 5 mg NAD+
- 20 ml of 0.5 M sodium lactate solution
- 40 ml tris-citrate buffer

Peptidase A (after Lewis and Harris, 1967, and Lewis and Truslove, 1969):
- 10 mg DL valyl-leucine
- 1 mg horseradish peroxidase
- 5 mg 0-dianisidine in 10 ml acetone
- 0.5 ml M $MgCl_2$
- 1 mg *Bothrops atrox* venom
- 40 ml tris-citrate buffer

Phosphoglucomutase (PGM) (after Spencer, Hopkinson, and Harris, 1964):
- 100 mg glucose-1-phosphate (dipotassium salt)
- 5 mg NADP
- 5 mg PMS
- 3 mg NBT
- 20 units glucose-6-phosphate dehydrogenase

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

TABLE 2.—Classification of species of Scorpaenidae into various groups by means of biochemical characteristics.

Species	Biochemical characteristics						Biochemical group
	Muscle pattern[1]	TO	GPDH	LDH	Peptidase A		
					I (Fast zone)	II (Slow zone)	
Pacific *Sebastes*							
S. elongatus	2	F	E	C	c	c	I[2]
S. entomelas	2	S	E	C	c	c	II[2]
S. aurora	3	F	E	C	b	d	III[2]
S. chlorostictus	4	F	E	B	a	c	IV[2]
S. aleutianus	4	F	E	C	c	c	V
S. zacentrus	4	F	E	C	c	c	V
S. caurinus	4	F	F, S	C	d	c	VI
S. diploproa	4	F	E	C	b	b	VII[2]
S. helvomaculatus	4	F	E	B	c	c	VIII[2]
S. maliger	4	F	F	C	d	c	VI
S. ruberrimus	4	F	E	C	c	c	V
S. rubrivinctus	4	F	E	C	c	c	V
S. saxicola	4	F	F	C	c	c	IX[2]
S. auriculatus	4	F	E, F	C	d	c	VI
S. brevispinis	4	F	E	C	c	c	V
S. flavidus	4	S	E	C	c	c	X
S. melanops	4	S	E	C	c	c	X
S. pinniger	4	S	E	C	c	c	X
S. proriger	4	S	E	C	c	c	X
S. wilsoni	4	S	--	--	--	--	--
S. variegatus	4	S	E	C	a	c	XI[2]
S. caenaematicus	4	S	E	C	c	c	X
S. alutus	4	S	F, S	C	c	c	XII[2]
S. crameri	4	VS	E	C	c	c	XIII
S. paucispinis	4	VS	E	C	c	c	XIII
S. reedi	4	VS	E	C	c	c	XIII
S. levis	—[3]	F	E	C	a	c	XIV[2]
Sebastolobus alascanus	A	VS	D	A	b	a, e	XV[2]
Atlantic *Sebastes*							
S. marinus	B	S	E, F	B	c	c	XVI
S. viviparous	B	S	E	B	c	c	XVI
Helicolenus dactylopterus	G	S, VS	C	B	e	b	XVII[2]

[1] Modified after Tsuyuki et al., 1968.
[2] Species with unique biological characteristics.
[3] Pattern of the single specimen tested has not been described.

0.5 ml 1 M $MgCl_2$
40 ml tris-citrate buffer

Isocitrate dehydrogenase (ICDH):

(a) NADP dependent (after Opher, Leonard, and Miller, 1969):
30 mg DL sodium isocitrate
5 mg NADP
0.5 ml 1 M $MgCl_2$
5 mg PMS
5 mg NBT
40 ml tris-citrate buffer

(b) NAD + dependent:
Same formulation as NADP dependent, but substituting 10 mg NAD+ for 5 mg NADP

Muscle protein detected by nonspecific protein staining using 1% nigrosin-buffalo black in solution of 1:4:5 acetic acid:methanol:water and destained with a 1:4:5 solution of acetic acid, methanol, and water.

ENZYME AND PROTEIN PHENOTYPES

TETRAZOLIUM OXIDASE (TO)

Interspecific variation of TO was previously reported in the genus *Sebastes* (Pacific) by Johnson et al. (1970b), where three anodal mobilities were observed in 15 species studied: Fast (F), Slow (S), and Very Slow (VS). These findings are expanded in the present study (Table 2, Figure 1). The F band occurred in 15 of the 27 Pacific *Sebastes* species; the S band was present in 9 species and the VS band in 3 species. Only the S band occurred in both Atlantic *Sebastes* species. The VS band was found

FIGURE 1.—Band in starch-gel illustrating the four tetrazolium oxidase phenotypes, F, S, S-VS, and VS, detected in the family Scorpaenidae. The following samples are shown: 1, 5 *Helicolenus dactylopterus* (S-VS), 2 *Sebastes reedi* (VS), 3 *Sebastes caurinus* (F), 4 *Sebastes alutus* (S), and 6 *Sebastes reedi* (VS).

in *Sebastolobus alascanus*.[4] *Helicolenus dactylopterus* was polymorphic for the S and VS bands; of the 10 samples tested, two exhibited a three-banded phenotype having the S and VS bands in addition to another band of intermediate mobility, whereas the rest had only the single S band. The three-banded phenotype suggests that two TO alleles are segregating in *Helicolenus* and that tetrazolium oxidase functions as a dimer in scorpaenids. This interpretation is consistent with TO polymorphisms observed in salmonids (Utter, 1971) where three-banded phenotypes were observed in heterozygous rainbow trout (*Salmo gairdneri*) and chinook salmon (*Oncorhynchus tshawytscha*).

L-ALPHA -GLYCEROPHOSPHATE DEHYDROGENASE (αGPDH)

Evidence for a polymorphic dimer having two alleles—Fast (F) and Slow (S)—were described in *S. alutus* (Johnson et al., 1970a). In addition to the F and S bands, three faster αGPDH bands have been observed among the scorpaenids that we have tested: E, D, and C,[5] listed according to increasing mobility (Figure 2 and Table 2). Additional αGPDH bands invariably occurred, regardless of phenotype, when electrophoresis proceeded beyond a 6-cm anodal migration of the dye marker. These bands are presumably artifacts of electrophoresis and did not alter our interpretation of enzyme variations. This phenomenon was also noticed by McCabe, Dean, and Olson (1970) in αGPDH variants of skipjack tuna (*Katsuwonus pelamis*).

In Pacific *Sebastes*, 19 species were monomorphic for the E band. *S. auriculatus* was polymorphic for the E and F bands. *S. caurinus* as well as *S. alutus* were polymorphic for F and S bands. *S. maliger* and *S. saxicola* were monomorphic for the F band. In the Atlantic *Sebastes*, *S. viviparous* was monomorphic for the E band and *S. marinus* was polymorphic for the E and F bands. The D and C bands were monomorphic *Sebastolobus alascanus* and *Helicolenus dactylopterus*, respectively.

[4] We used liver extracts of this species for detection of TO activity because muscle extracts failed to develop TO bands. We assume that this is a valid comparison because of parallel TO activity between liver and muscle observed in other scorpaenid species. All other scorpaenid enzymes tested were extracted from skeletal muscle.

[5] The separation of αGPDH bands C and D depends on optimal electrophoretic conditions.

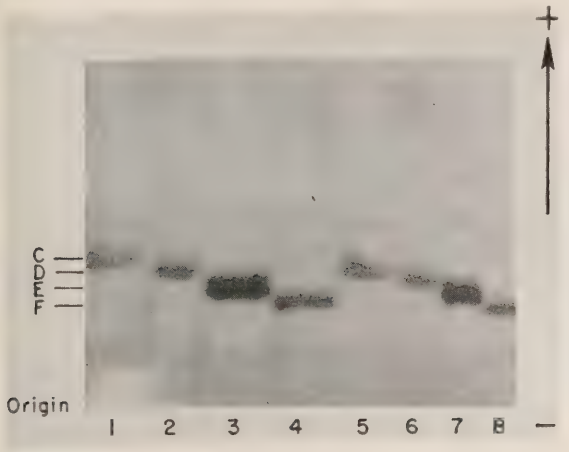

FIGURE 2.—Bands in starch-gel illustrating four L-alpha glycerophosphate dehydrogenase phenotypes (C, D. E, F) detected in the family Scorpaenidae. The following samples are shown: 1, 5 *Helicolenus dactylopterus* (C), 2, 6 *Sebastolobus alascanus* (D), 3, 7 *Sebastes rubrivinctus* (E), and 4, 8 *Sebastes alutus* (F).

LACTIC DEHYDROGENASE (LDH)

Muscle LDH was resolved as a single anodal band in each scorpaenid species we tested. This agrees with studies of Wilson, Kitto, and Kaplan (1967), who found single anodal bands of muscle LDH in two scorpaenid species, *Sebastes marinus* and *Scorpaenopsis gibbosa.* The electrophoretic mobilities were distinct in each species. LDH bands of three different mobilities (A, B, and C) were found in our sampling (Figure 3 and Table 2). No polymorphisms were detected. All but two Pacific *Sebastes* species expressed the C band. The B band was found in *S. helvomaculatus* and *S. chlorostictus.* The B band was found in two Atlantic *Sebastes* species and *Helicolenus dactylopterus.* Only *Sebastolobus alascanus* expresses the LDH A band.

PEPTIDASE

Peptidase staining occurred in two anodal regions for all species tested (Figure 4, Table 2). Both regions are developed with the dipeptide valyl-leucine, which is the specific substrate for peptidase A in mammals (Lewis and Harris, 1967; Lewis and Truslove, 1969). We have therefore called these regions peptidase A-I and peptidase A-II.

FIGURE 3.—Bands in starch-gel illustrating the three phenotypes of lactate dehydrogenase detected in the family Scorpaenidae. The following species are shown: 1, 4 *Sebastolobus alascanus* (A), 2, 5 *Sebastes helvomaculatus* (B), and 3, 6 *Sebastes alutus.*

Five different bands (a, b, c, d, e) were observed in the peptidase A-I (fast) zone. In Pacific *Sebastes,* peptidase A-I bands were expressed as follows: I^a - *S. chlorostictus, S. levis,* and *S. variegatus*; I^b - *S. caurinus, S. auriculatus,* and *S. maliger. S. marinus* had band I^c as did 9 of the 10 *S. viviparous* tested; *Sebastolobus alascanus* had band I^b; and *H. dactylopterus* had band I^e. The aberrant *Sebastes viviparous* sample had a single I^d band but corresponded to *S. viviparous* in all other systems tested. The significance of the variant is unclear. It may reflect an intraspecies genetic variant (although multiple bands would be expected if this were the case) or perhaps a sibling species. Because only muscle samples were available for Atlantic *Sebastes,* identification of subtle morphological differences between individuals was not possible.

Bands of five different mobilities (a, b, c, d, e) were also observed in the peptidase A-II (slow) zone. Band II^c was expressed in all but two Pacific *Sebastes* tested; band II^d was found in *S.*

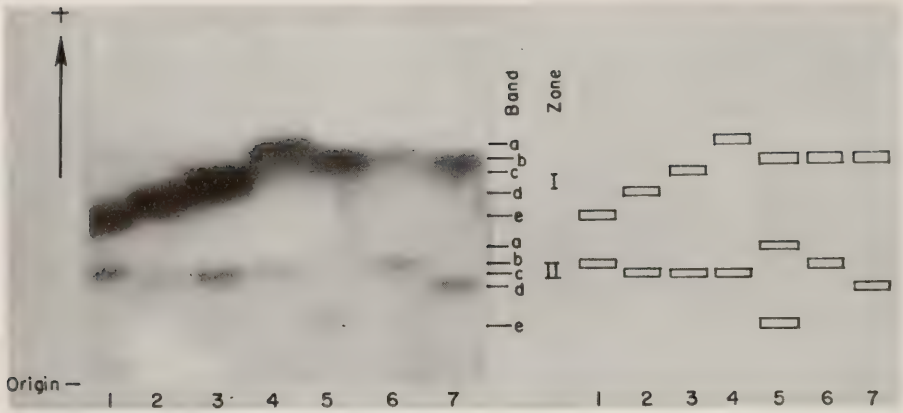

FIGURE 4.—Bands in starch-gel illustrating the various phenotypes of Peptidase A detected in the family Scorpaenidae. The following species are shown: 1 *Helicolenus dactylopterus* (II^b, I^e), 2 *Sebastes caurinus* (II^d, I^c), 4 *Sebastes variegatus* (II^c, I^a), 5 *Sebastologus alascanus* ($II^{a,e}$ I^b), 6 *Sebastes diploproa* (II^b, I^b), and 7 *Sebastes aurora* (II^d, I^b).

aurora and band II^b in *S. diploproa*. Band II^c was found in both Atlantic *Sebastes* species, and *Helicolenus dactylopterus* possessed band II^b. Two bands representing the extremes of peptidase A-II mobilities—II^a and II^e—were expressed in all *Sebastolobus alascanus* individuals tested. These bands are presumed to be fixed rather than polymorphic because of their invariant expression and may reflect gene duplication.

PHOSPHOGLUCOMUTASE (PGM)

PGM polymorphism was reported in *Sebastes alutus*, where two allelic bands—A and B—were described (Johnson, Utter, and Hodgins, 1971). In extending these observations here to additional scorpaenid species a third band—A′—has also been found which migrates somewhat faster than the A band (Figure 5).

PGM is the most polymorphic of the scorpaenid enzymes that we have investigated (Table 3). In Pacific *Sebastes* polymorphism was found in 10 species for the A and B bands and in 1 species for the A and A′ bands. Twelve species of Pacific *Sebastes* were monomorphic for the A band, one for the B band, and one for the A′ band. In other scorpaenid species, *Sebastes marinus* was polymorphic for the A and B bands, and *S. viviparous* was monomorphic for

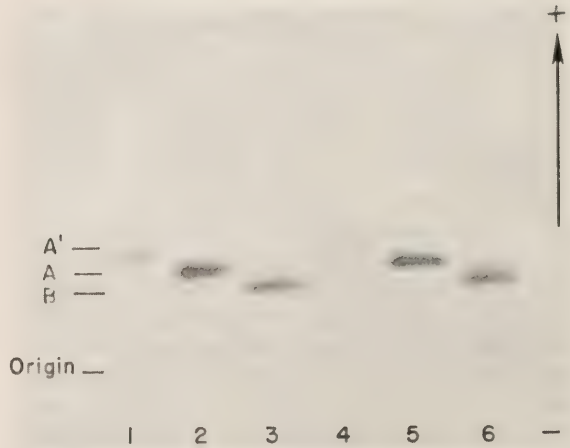

FIGURE 5.—Bands in starch-gel illustrating three mobilities of phosphoglucomutase detected in the family Scorpaenidae. The following species are shown: 1, 4 *Sebastolobus alascanus* (A′), 2, 5 *Sebastes caurinus* (A), and 4, 6 *Sebastes reedi* (B).

the A band. *H. dactylopterus* was polymorphic for the A and B bands, and *Sebastolobus alascanus* was monomorphic for the A′ band. We assume that these variants reflect allelic differences although further study is needed for some species. Also, the limited number of samples

tested for some species that were listed as monomorphic are too few to preclude the possibility of polymorphism.

ISOCITRATE DEHYDROGENASE, NADP DEPENDENT (ICDH NADP)

We tested for both NAD- and NADP-dependent ICDH in the 31 species studied and found activity only for the latter form. It is assumed that this represents cytoplasmic ICDH activity (Opher et al., 1969). Two anodal mobilities of ICDH were detected: the band of *H. dactylopterus* migrated slightly faster than the band of the other species (Figure 6). No activity was detectable in extracts of *Sebastolobus alascanus*. Activity was highly labile in all species, requiring testing on the same day that the extraction was made. It may be that *S. alascanus* has an even more labile form of ICDH than the other species tested.

TABLE 3.—Phosphoglucomutase phenotypes in muscle samples from species of Scorpaenidae.[1]

Species	Phenotypes				
	B	AB	A	AA′	A′
Pacific *Sebastes*					
S. aleutianus	--	+	+	--	--
S. alutus	+	+	+	--	--
S. auriculatus	--	--	+	--	--
S. aurora	--	+	+	--	--
S. brevispinis	+	+	+	--	--
S. caurinus	--	--	+	--	--
S. chlorostictus	--	--	--	--	+
S. crameri	--	+	+	--	--
S. elongatus	+	+	+	--	--
S. entomelas	--	--	+	--	--
S. flavidus	--	--	+	--	--
S. helvomaculatus	--	--	+	+	+
S. levis	--	--	+	--	--
S. maliger	--	--	+	--	--
S. melanops	--	--	+	--	--
S. paucispinis	--	+	+	--	--
S. pinniger	--	+	+	--	--
S. proriger	+	+	+	--	--
S. reedi	+	--	--	--	--
S. ruberrimus	--	--	+	--	--
S. rubivinctus	--	--	+	--	--
S. saxicola	--	--	+	--	--
S. zacentrus	--	--	+	--	--
S. caenaematicus	--	+	+	--	--
S. variegatus	--	--	+	--	--
Atlantic *Sebastes*					
S. marinus	--	+	+	--	--
S. viviparous	--	--	+	--	--
Sebastolobus alascanus	--	--	--	--	+
Helicolenus dactylopterus	+	--	+	--	--

[1] PGM in our samples of *S. diploproa* and *S. wilsoni* did not develop.

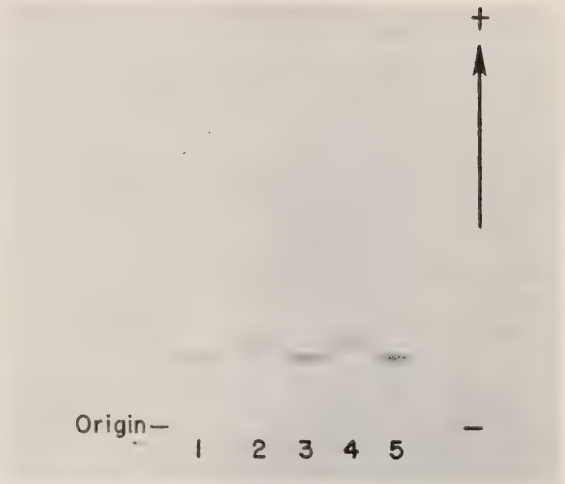

FIGURE 6.—Isocitric dehydrogenase (NADP dependent) bands found in the family Scorpaenidae. Samples 1, 3, 5 are *Sebastes alutus* and samples 2, 4 are *Helicolenus dactylopterus*.

MUSCLE PROTEIN

A satisfactory separation of muscle protein bands was obtained by permitting the dye marker to migrate 9.0 cm anodally from the origin. These bands were separated into two regions—A and B (Figure 7).

Distinct protein patterns occurred in region A, which differ between genera as well as within the genus *Sebastes* (Pacific) (Table 4). *S. aurora* has a unique pattern (bands 1, 4) which differed from the other Pacific *Sebastes* species (bands 1, 3). The intergeneric differences in region A were: *Sebastes* (Pacific)—bands 1, 4 and 1, 3; *Sebastes* (Atlantic)—bands 2, 6; *Helicolenus*—bands 3, 7; and *Sebastologus*—5, 7. A band (X) which migrated more anodally than band 7 was found in some *Sebastes alutus*. We assume this band (X) to be an artifact as it did not appear in repeated tests. The most anodal band (8) was found in all samples tested. Corresponding region A patterns were not described by Tsuyuki et al. (1968) in instances where the same species were tested and may arise from differences in methodology such as buffer systems (Rasmussen, 1969).

TABLE 4.—Intergeneric comparison of muscle protein bands of Scorpaenids.

Genus	Subgroup[1]	Protein bands																						
		Region B[2]																Region A						
		a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	1	2	3	4	5	6	7	8
Pacific *Sebastes*	2	+	+	+	--	--	--	--	--	--	+	+	--	+	--	--	+	+	--	+	--	--	--	--	+
Pacific *Sebastes*	3	--	--	--	--	--	+	--	+	--	--	+	--	+	--	--	+	+	--	--	+	--	--	--	+
Pacific *Sebastes*	4	+	+	+	--	--	--	--	--	+	--	+	--	+	--	--	+	+	--	+	--	--	--	--	+
Atlantic *Sebastes*	--	+	+	+	--	--	--	--	--	+	--	+	--	+	--	--	+	--	+	--	--	--	+	--	+
Sebastolobus	--	--	--	--	--	--	--	--	--	+	--	--	+	--	--	+	--	--	--	--	--	+	--	+	+
Helicolenus	--	+	+	+	--	--	--	--	--	+	--	+	--	+	--	--	+	--	--	--	--	--	--	+	+

[1] Pacific *Sebastes* subgroups after Tsuyuki et al., 1968.
[2] Alphabetical classification after Tsuyuki et al., 1968.

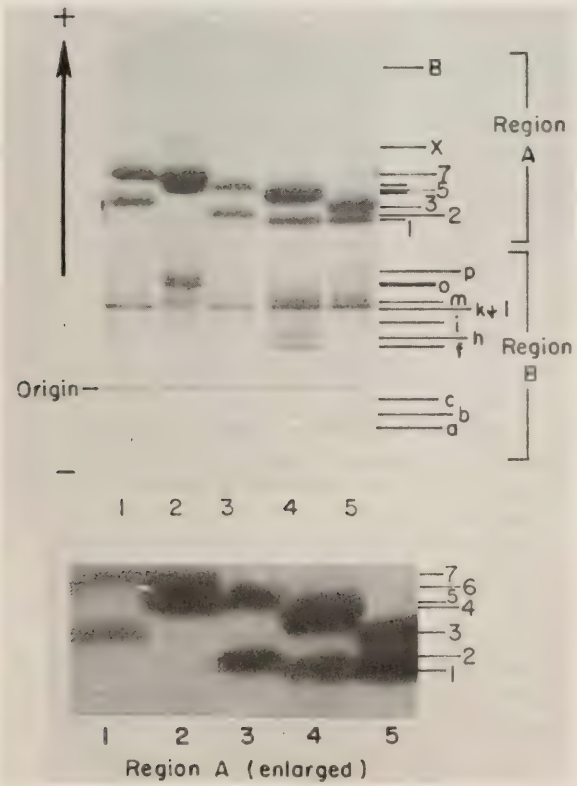

FIGURE 7.—Muscle protein bands in starch-gel: 1 *Helicolenus dactylopterus* (A-3, 7), 2 *Sebastolobus alascanus* (A-5, 7), *Sebastes marinus* (A-2, 6), 4 *Sebastes aurora* (A-1, 4), and 5 *Sebastes alutus* (A-1, 3).

The protein patterns in region B were similar to those described by Tsuyuki et al. (1968), who described 16 bands (a-p) that varied between genera and species. Three cathodally migrating bands (a, b, c) occurred in Pacific *Sebastes* (except *S. aurora*), Atlantic *Sebastes*, and *Helicolenus*. Bands b and c stained weakly in our gels and failed to show in some individuals (Figure 7). The slowest anodal bands were f and h which occurred only in *S. aurora*. Band i occurred in all species tested except *S. aurora*, *S. elongatus*, and *S. entomelas*. On the other hand, *S. entomelas* and *S. elongatus* were the only species having the j band, bands j and k being polymorphic in *S. elongatus* (first reported by Tsuyuki et al., 1968). Band k was present in all genera but *Sebastolobus*, which—in turn—was the only genus expressing band l. Similarly, bands m and p—present in other genera—were absent in *Sebastolobus*, which uniquely expressed band o. Our methods were unable to detect band q, reported by Tsuyuki et al. in Atlantic *Sebastes* and *Sebastolobus*.

COMPARISON OF VARIATION BETWEEN GENERA

A comparison of the total variation between genera suggests some possible relations. The greatest similarity was between the Pacific *Sebastes* and Atlantic *Sebastes* where all the electrophoretic patterns of the Atlantic *Sebastes* were found in one or more species of the Pacific *Sebastes*, except for the protein bands of region A. Pacific *Sebastes* and *Sebastolobus* exhibited common bands for PGM, TO, peptidase A-I, and protein B-i. Pacific *Sebastes* and *Helicolenus* shared common bands for LDH, PGM, and protein bands of region B. *Helicolenus* and one species of Pacific *Sebastes* possessed a common peptidase A-II band. *Helicolenus* and *Sebastes* had common bands in LDH, PGM, and protein region B. *Helicolenus* and *Sebastolobus* shared only pro-

tein bands B-i and A-7. Only protein band B-i was common to *Sebastolobus* and the Atlantic *Sebastes* (Tables 2, 4, and 5).

When the total amount of common patterns between genera is considered, we agree with Tsuyuki et al. (1968) that there is relatively greater similarity between the Pacific *Sebastes* and the Atlantic *Sebastes* than between either and the other genera studied. *S. aurora* was found to have relatively the same degree of difference between itself and the other Pacific *Sebastes* species as there was between the Atlantic *Sebastes* and the Pacific *Sebastes*. This agrees with the findings of Tsuyuki et al. (1968) who suggested that *S. aurora* should possibly be elevated to the generic level because of its degrees of difference. The interpretation of similarity based on electropherograms must be done with caution as only amino acid substitutions which change the net charge of the polypeptide chain can be detected.

TABLE 5.—Summary of intergeneric enzymatic similarity in Scorpaenidae.[1] X indicates the occurrence of common bands between one or more species of the genera compared.

Genus and enzyme	Genera			
	Pacific *Sebastes*	Atlantic *Sebastes*	*Sebastolobus*	*Helicolenus*
Pacific *Sebastes*				
TO		X	X	--
αGDPH		X	--	--
LDH		X	--	X
Peptidase A-I		X	X	--
Peptidase A-II		X	--	X
ICDH		X	--	--
PGM		X	X	X
Atlantic *Sebastes*				
TO	X		--	--
αGDPH	X		--	--
LDH	X		--	X
Peptidase A-I	X		--	--
Peptidase A-II	X		--	--
ICDH	X		--	--
PGM	X		--	X

[1] No common bands were found between *Sebastolobus* and *Helicolenus*.

VARIATION WITHIN PACIFIC *SEBASTES*

Combining the enzyme and protein variations in the Pacific *Sebastes* resulted in 10 of the 27 Pacific *Sebastes* species having unique biochemical profiles (Table 2). These species were *S. elongatus*, *S. entomelas*, *S. aurora*, *S. chlorostictus*, *S. diploproa*, *S. helvomaculatus*, *S. saxicola*, *S. variegatus*, *S. alutus*, and *S. levis*. Some species were represented by only a few samples —therefore further sampling may reveal variation in these profiles. PGM was not included in these profiles because of its high degree of polymorphism in the genus. A new species, *S. reedi*, was reported by Westrheim and Tsuyuki (1967) that resembles *S. crameri*, *S. alutus*, and *S. proriger* but was readily separable from these when morphology and biochemical methods were employed. Our study found that *S. reedi* and *S. crameri* were identical with respect to muscle protein and five enzyme systems but differed in PGM. This suggests that *S. reedi* may be more closely related to *S. crameri* than to the other species.

Three species, *S. caurinus*, *S. maliger*, and *S. auriculatus*, had profiles that differed only in the enzyme αGPDH, which was monomorphic in *S. maliger* (F band) but polymorphic for the F and S bands in *S. caurinus*. All three species have the peptidase A-I[d] band which was found in no other *Sebastes* species. These three species are very similar in morphology and habitat preferences. In certain areas of Puget Sound, Wash., hybridization between the three may occur, whereas in other areas they remain separate because of behavioral differences.[6] Investigation of biochemical and morphological characteristics of these species may provide valuable information on the processes of speciation.

The amount of polymorphism of αGPDH and PGM in the family Scorpaenidae could prove to be useful for the identification of breeding populations and verification of species and subspecies. On the basis of morphometric data, Barsukov (1964) suggested that two subspecies exist in *Sebastes alutus* (*S. a. alutus*—off the Pacific coast of North America and *S. a. paucispinus*—from Honshu Island, Japan, to perhaps Bristol Bay, Alaska). Westrheim (1970) suggested that *S. alutus* had a southern and a northern type of fish off the coast of North America—the south-

[6] C. R. Hitz, National Marine Fisheries Service, Fishery Biologist, Exploratory Fishing and Gear Research Base, Seattle, Wash., personal commun., April 1971.

ern type south of Dixon Entrance and the northern type North of Dixon Entrance and in the Gulf of Alaska. Differences in gene frequencies would add to the support of their separations. This approach may also prove useful in studying complexes such as found in *S. aleutianus, S. reedi,* and *S. diploproa* (Tsuyuki et al., 1968).

SUMMARY

An investigation of muscle protein and six enzymatic systems by starch-gel electrophoresis was presented. Samples of 31 species of three genera of the family Scorpaenidae were compared which resulted in the conclusion that a relatively greater similarity existed between the Pacific *Sebastes* and the Atlantic *Sebastes* than between the other genera.

Ten of the 27 species of Pacific *Sebastes* had unique profiles when the systems were compared.

ACKNOWLEDGMENTS

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THE SYNERGISTIC EFFECTS OF TEMPERATURE, SALINITY, AND MERCURY ON SURVIVAL AND METABOLISM OF THE ADULT FIDDLER CRAB, *UCA PUGILATOR*[1]

WINONA B. VERNBERG AND JOHN VERNBERG[2]

ABSTRACT

Gill tissues of fiddler crab, *Uca pugilator*, were the major site of mercury concentration; lesser amounts accumulated in the hepatopancreas and green gland. Very small amounts were found in the carapace and muscle tissue. No significant differences in the amount of mercury in tissues of males and females were found.

A concentration of mercury sublethal to fiddler crabs under optimum conditions of temperature and salinity greatly reduced survival times when crabs were placed under conditions of temperature and salinity stress. Males were more susceptible to the synergistic effects of mercury in combination with environmental stress than were females.

Metabolic rates of male and female fiddler crabs were affected by prolonged exposure to mercury both under optimum environmental conditions and under temperature and salinity stress. Metabolic rates of males were more adversely affected than those of females.

Estuaries are an extremely important part of the marine environment. Yet often an estuary becomes so grossly polluted that much of the biota is destroyed before it is recognized that the quality of water affects the biology of such an area. Part of the problem is the subtleness of the effects of sublethal concentrations of man-introduced pollutants. In low concentration the pollutant may have no observable effect on a given population of animals if environmental conditions remain at an optimum. However, when another environmental parameter becomes stressful, it may synergistically interact with the sublethal concentration of pollutant and the organism dies. Many estuaries are polluted, and since one of the chief characteristics of estuaries is the rather extreme environmental fluctuations that occur throughout the year, knowledge of synergistic interaction on estuarine animals is important in the preservation of estuarine ecosystems.

This study was undertaken to determine the effect of a sublethal concentration of mercury on the metabolism of adult male and female fiddler crabs, *Uca pugilator* (Bosc), maintained under optimum and stressful conditions of temperature and salinity, and the synergistic effects on survival of this species with sublethal concentration of mercury in combination with salinity and thermal stress. This species was selected because it is one of the more abundant and ecologically important species in an estuarine ecosystem.

MATERIALS AND METHODS

Crabs used in this study were collected in the Georgetown, S.C., area during the fall and winter months. After collection the animals were brought into the laboratory where they were maintained in plastic boxes containing a thin layer of seawater having a salinity of approximately 30‰. All crabs were kept in constant temperature boxes at 25°C and on a 12-hr light-dark photoperiod for at least 2 weeks. Crabs were fed on Clark's fish pellets every third

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day; the water was changed after each feeding. Preliminary studies were undertaken to determine the amount of $HgCl_2$, an inorganic mercury compound, that could be added to the water without killing the crabs. A concentration of 9×10^{-7} M $HgCl_2$ was found to be sublethal for crabs which were kept under optimal conditions of temperature and salinity. Under these conditions crabs survived for a 2-month period with only slight mortality. The experiment was terminated at this point. The initial concentration of mercury, 9×10^{-7} M $HgCl_2$ was 0.18 ppm Hg (or 0.18 mg/liter seawater).

Tissues of crabs were analyzed for mercury following exposure to 0.18 ppm mercury in 30‰ seawater at a temperature of 25°C for 1, 3, 7, 14, and 28 days. Tissues of crabs maintained under the same conditions but without added mercury were also analyzed. Tissues were removed from 10 crabs for each assay and frozen immediately. The concentration of mercury in each tissue was then determined on a Perkin-Elmer Mercury Analyzer System-50.[3] The techniques were based on the Environmental Protection Agency method developed by the Analytical Quality Control Laboratory, using dilute nitric acid to digest the samples. Determinations were made by South Carolina State Board of Health personnel. Five tissues were assayed: gill, hepatopancreas, green gland, abdominal muscle, and carapace. None of the tissues were kept frozen for more than 1 week. Tissues from 20 males and females (two determinations each) were assayed for each of the five experimental time exposures. Since the amount of mercury proved to be essentially the same in tissues of both males and females, all data were pooled.

To determine the synergistic effects of the normally sublethal concentrations of mercury and stressful environmental factors, crabs acclimated to 25°C, 30‰ seawater were placed in seawater with a salinity of 5‰ containing 0.18 ppm mercury or in 5‰ seawater without mercury and maintained at either 5°C or 35°C. At each experimental temperature, four groups of animals were used. Thus at 5°C, 5‰, one group of 30 males and a second group of 30 females were used as controls; in the experimental group 30 males and 30 females were maintained under the same conditions except the water contained 0.18 ppm mercury. The same procedure was followed at 35°C and in a salinity of 5‰. Survival of both experimental and control crabs was followed for 28 days or until 50% of any one group had died. The temperatures of 5°C and 35°C were selected since they represent low and high temperature extremes which fiddler crabs experience seasonally in South Carolina marshes. A salinity of 5‰ is also encountered by them in the field.

Oxygen consumption of control and experimental animals was determined by means of a Gilson respirometer using respiration flasks with a volume of approximately 140 cc. Base-line oxygen consumption measurements were made on 10 males and 10 females in untreated seawater (30‰) at 25°C. These same crabs were then maintained under the same conditions but with 0.18 ppm Hg added to the water, and metabolic determinations made on days 1, 3, 7, 14, 21, and 28. Only medium-sized crabs in the intermolt stage were used to avoid any variation due to molting or metabolic size relationships.

Oxygen consumption rates were also determined on crabs exposed to mercury in combination with temperature and salinity stress. Metabolic measurements were made on crabs maintained in 5‰ seawater at 5°C (control crabs) and crabs kept in 5‰ seawater at 5°C with 0.18 ppm Hg added to the water (experimental crabs). Oxygen consumption rates were then determined after 1 and 3 days exposure for experimental crabs and 1, 3, and 7 days for control crabs. These conditions proved too stressful for most of the crabs to survive longer periods of time. The same experimental procedures were followed for crabs kept in 5‰ at 35°C with and without added mercury. Since these conditions were less stressful than the combination of low salinity and low temperature, it was possible to measure the metabolic rate of these crabs on days 1, 3, 7, 14, and 21 for experimental animals and to day 28 for control crabs. All results are expressed as μliters of oxygen consumed per hour per gram live weight.

[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

RESULTS

MERCURY UPTAKE BY TISSUE

Mercury was not detected in the untreated seawater, although there were detectable traces of mercury found in the Clark's fish pellets fed to the crabs. The hepatopancreas of the control animals (animals collected in the same region as experimental animals and maintained in seawater without mercury addition) had approximately 0.03 ppm mercury, but no mercury was found in any of the other tissues. Within the first 24 hr after exposure to 30‰ seawater at 25°C containing an initial concentration of 0.18 ppm mercury, however, gill tissue contained 1.73 ppm mercury; the amount of mercury in this tissue increased steadily with continued exposure (Figure 1). Of the five tissues assayed for mercury content, gill tissue was found to have the highest concentration. Mercury also accumulated in the hepatopancreas and green gland although much less rapidly and at a lower concentration level (Figure 1). Lower amounts of mercury were found in abdominal muscle tissues and in the carapace; after 28 days exposure to water containing mercury, levels were approximately 1 ppm.

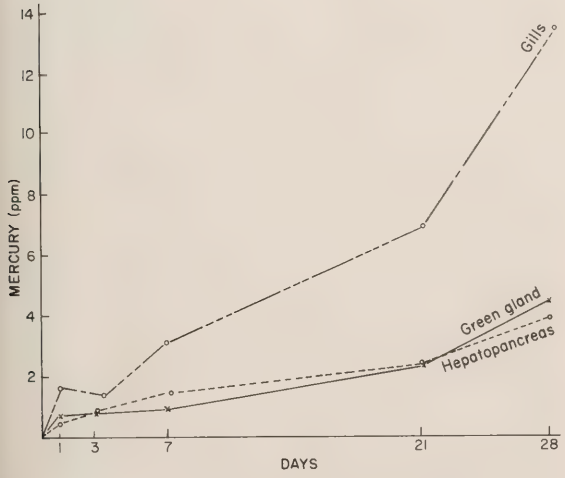

FIGURE 1.—Mercury in tissues of *Uca pugilator* after exposure of the crabs to 9×10^{-7} M $HgCl_2$ (0.18 ppm Hg) in 30‰ seawater at 25°C for varying lengths of time.

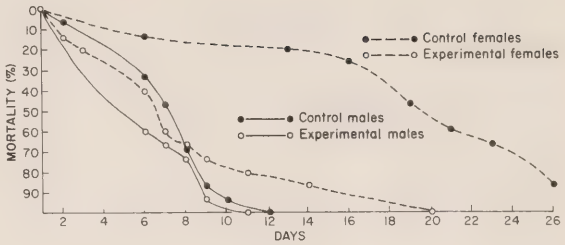

FIGURE 2.—Mortality of *Uca pugilator* in 5‰ seawater at 5° C with and without the addition of 9×10^{-7} M $HgCl_2$ (0.18 ppm Hg).

LETHAL LEVELS

Preliminary studies established that under optimum conditions of temperature (25°C) and salinity (30‰) the crabs could survive for prolonged periods of time (at least 2 months) in seawater having an initial concentration of 9×10^{-7} M $HgCl_2$ (0.18 ppm mercury). Under temperature and salinity stress, however, this concentration of mercury significantly shortened survival time. For example, under conditions of low temperature (5°C) and low salinity (5‰), such as could occur following heavy winter rains, the crabs could not survive as long as under conditions of high temperature and low salinity. In winter animals without the added stress of a pollutant, 50% of the females survived 21 days but 50% of the males were dead within 7 days. Under the same temperature and salinity conditions with the addition of 0.18 ppm mercury, males survived 6 days, but 50% of the females died by day 8 (Figure 2). Under conditions of low salinity (5‰) and high temperature (35°C), conditions very apt to occur following the heavy rains associated with a summer hurricane, both male and female *U. pugilator* can survive with very little mortality for at least 28 days (Figure 3). With the addition of 0.18 ppm mercury, however, survival times of both males and females are reduced. Under conditions where crabs were maintained at this high temperature and low salinity in water containing mercury, 50% of the males had died by day 17, while 50% of the females survived to day 26 (Figure 3).

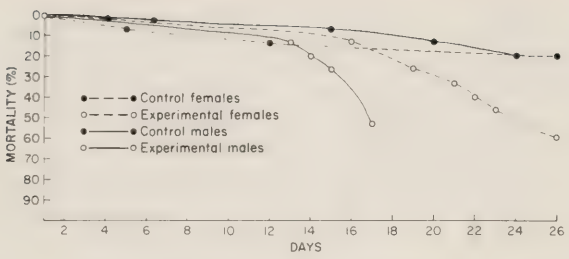

FIGURE 3.—Mortality of *Uca pugilator* in 5‰ seawater at 35°C with and without the addition of 9×10^{-7} M $HgCl_2$ (0.18 ppm Hg).

METABOLIC EFFECTS

Although a low level concentration of mercury was not lethal to the crabs under optimum environmental conditions, metabolic rates of these crabs were affected, especially those of males. Initially, metabolic rates were established for both males and females at 25°C in 30‰ seawater, and the rates for males and females were essentially the same (Figure 4). After the base-line rate was determined, the same animals were then maintained at 25°C in 30‰ seawater with the addition of mercury, and metabolism of the crabs was determined periodically for 28 days. The metabolic rate of the males remained essentially unchanged through day 3. By day 7, however, the metabolic rate had dropped to 32% of that of untreated crabs; by day 21 the rate had decreased by 48%; and by day 28 the rate was 20% lower than the base-line value. In the female, oxygen uptake values also decreased by day 7, but by day 14 the metabolic rate returned to the base-line rate and remained essentially at this level through day 28. Although initially the same, the rate of oxygen uptake of males was significantly lower than that of the females after 21 days in this sublethal concentration of mercury, and the metabolic rate of the males had not returned to the same level as it was before the crabs were placed in mercury by the end of the 28 day experimental period (Figure 4). Both males and females, however, continued to survive for another month under the same mercury regime as before without any significant increase in mortality.

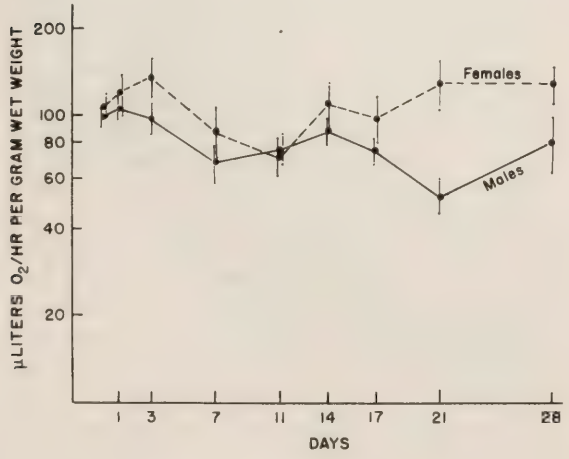

FIGURE 4.—Oxygen uptake rates of male and female *Uca pugilator* maintained in 30‰ seawater containing 9×10^{-7} M $HgCl_2$ (0.18 ppm) at 25°C. The base-line rate is represented by the first set of data points on the left. The vertical bar through each mean value is the standard error.

Under conditions of low temperature (5°C) and salinity (5‰) stress, not only did females survive much longer than males, but also the females were better able to maintain a steadier rate of oxygen uptake (Figure 5). The metabolic rate and pattern of the experimental female crabs were similar to those of the control female crabs. The metabolic rate of male experimental crabs was not significantly different from that of the female experimental or male and female control crabs, after a 1-day exposure to mercury, but by day 3 the rate dropped markedly (Figure 5).

Oxygen uptake rates of female control crabs maintained in low-salinity water (5‰) and at high temperature (35°C) were relatively constant over a 28-day period and tended to be higher than that of control male crabs (Figure 6). The metabolic rates of experimental female crabs remained fairly constant for the first 7 days and then declined rapidly. The uptake rates of experimental male crabs declined steadily from day 1 and tended to be lower than those of the females throughout the remainder of the time period (Figure 6).

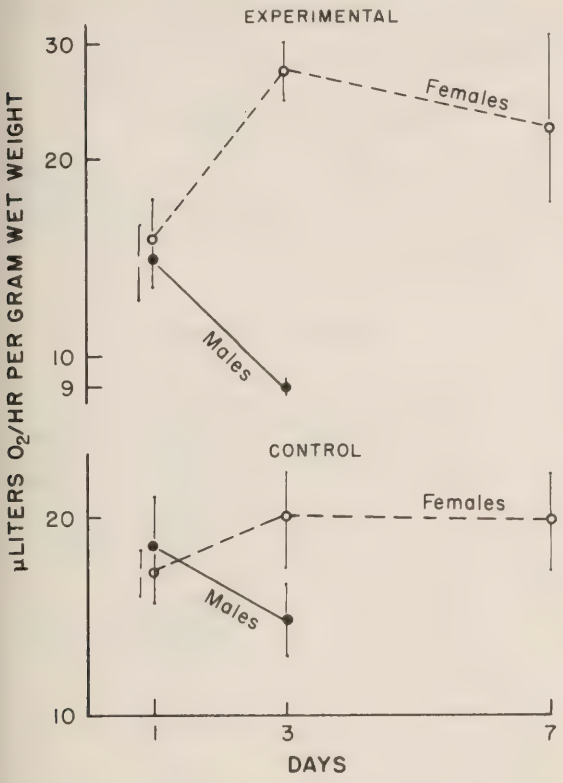

FIGURE 5.—Oxygen uptake rates of male and female *Uca pugilator* maintained at 5° in 5‰ seawater with and without the addition of 9×10^{-7} M $HgCl_2$ or 0.18 ppm. The vertical bar through each mean value is the standard error.

DISCUSSION

Fiddler crabs are capable of rapidly removing mercury from their surrounding aqueous media and retaining it in their tissues. However, not all tissues concentrate mercury to the same degree. The rapid accumulation and large concentration of mercury in gill tissue of fiddler crabs and the lesser but significant amounts of mercury found in the hepatopancreas and green gland are similar to results obtained in experiments involving other heavy metals. Bryan (1966), for example, found the highest concentration of zinc in the gills and hepatopancreas. He related these concentrations to the fact that excess zinc can be stored in the hepatopancreas in the crab *Carcinus maenus* and concentrated and excreted across the gills.

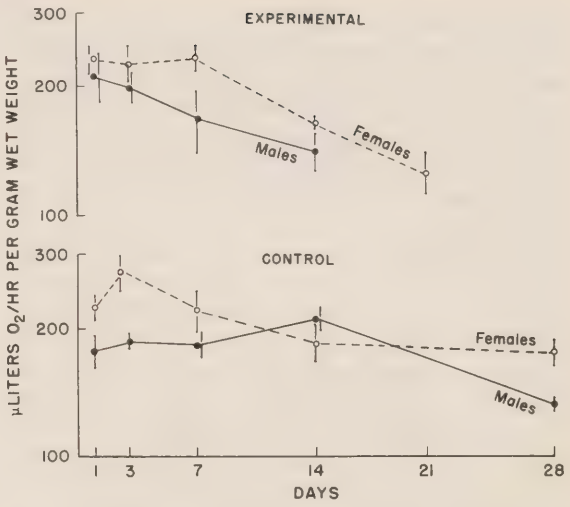

FIGURE 6.—Oxygen uptake rates of male and female *Uca pugilator* maintained at 35°C in 5‰ seawater with and without the addition of 9×10^{-7} M $HgCl_2$ or 0.18 ppm. The vertical bar through each mean value is the standard error.

Uca pugilator can adapt quickly to a wide range of adverse environmental fluctuations (Vernberg and Vernberg, 1970). The sudden changes in temperature and salinity that do occur usually do not persist for prolonged periods of time, and conditions usually ameliorate within a week or two. Results presented in this paper indicate that the crabs can withstand low salinity and high temperature better than low salinity coupled with low temperature, findings consistent with the earlier generality proposed by Panikkar (1940). Further, Lockwood (1962) stated that since ionic regulation is thermally influenced, organisms survive dilute medium more successfully when the rate of ion uptake as compared with ion loss increases faster with increasing temperature. Under both sets of conditions, however, the added stress of concentrations of mercury that are sublethal under optimum conditions adversely affected survival rates under stressful conditions and more markedly in males than in females. Bryan (1971) has speculated that the increased lethality of a heavy metal under stressful conditions is in some way related to changing rates of absorption. Our data are another example of the principle

that multiple environmental factors, each at a sublethal level, interact synergistically to cause death. Earlier papers, especially the classic paper of McLeese (1956), emphasized the lethal role of "normal" environmental factors, whereas we have demonstrated the importance of pollutants as part of the "normal" environment of many species.

Under optimal conditions of temperature and salinity mercury generally decreased metabolic rates of the males; effect on metabolic rates of females was much less pronounced. This differential effect of mercury on the metabolism of males and females is difficult to understand. On an interspecific basis, differences between resistance of larvae of *Artemia salina* and *Elminius modestus* to mercury have been related to differences between rates of uptake rather than of tissue resistance (Corner and Rigler, 1958). However, since the amount of mercury in tissues of both male and female fiddler crabs was essentially the same, these differences would not appear to be related to differences in uptake of the mercury. Under conditions of thermal and salinity stress without the addition of mercury the metabolic rate of the female crabs tended to be more stable and less depressed than the rate of male crabs. The addition of mercury to the already stressful conditions accentuated these differences.

Our results indicate, then, that a concentration of mercury that is sublethal under optimum conditions of temperature and salinity, may greatly reduce the ability of the population to survive under normally stressful conditions of temperature and salinity flux.

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LENGTH-WEIGHT RELATIONSHIP, FOOD HABITS, PARASITES, AND SEX AND AGE DETERMINATION OF THE RATFISH, *HYDROLAGUS COLLIEI* (LAY AND BENNETT)[1]

ALLYN G. JOHNSON[2] AND HOWARD F. HORTON[3]

ABSTRACT

In the fall and winter of 1965-1967, 292 ratfish (*Hydrolagus colliei*) were collected from four locations off the Pacific coast of Oregon. Specimens were examined for length-weight relationships, food habits, parasites, and a method of sex and age determination. Equations describing the body weight-body length (snout to vent) relationships were log weight = log −4.3217 + 3.0546 log length for males, and log weight = log −4.1692 + 2.9720 log length for females. The food organisms most important to ratfish were shrimp (*Pandalus* and *Crago*), mollusks (*Musculus* and *Amphissa*), and echinoderms (*Brisaster*). Two occurrences of cannibalism were found in ratfish collected off Cape Arago, Oreg. Infestations by *Gyrocotyle* ranged from 29 to 66% among samples from the four locations. The copepod, *Acanthochondria* sp., was attached to the claspers of seven males from Cape Arago. Eye-lens weights (wet and dry), vertebral radii, basal sections of the dorsal spine and left pectoral fin, and body-length frequencies were studied, but no accurate method of age determination was found. Tritors on the posterior side of the vomerine dental plate may be indicative of age, but the precise relationship was not determined.

The ratfish, *Hydrolagus colliei* (Lay and Bennett), is a member of the class Chondrichthyes, order Chamaeriformes, and family Chimaeridae (Bailey, 1970). Distributed from western Alaska to northern Baja California (Koratha, 1960), this cartilaginous fish is the only chimaeroid found on the Pacific coast of Canada and the United States. Ratfish are of little economic value, but their liver oil is an excellent lubricant and could be used commercially (Clemens and Wilby, 1961). Ratfish are an important source of food for such commercial fishes as soupfin sharks, *Galeorhinus zyopterus* (Nakatsu, 1957), spiny dogfish, *Squalus acanthias* (Alverson and Stansby, 1963), and Pacific halibut, *Hippoglossus stenolepis* (Thompson, 1915). Conversely, ratfish are commonly caught in the trawls of commercial fishermen who consider them a nuisance. Our study was conducted to help fill the need for more information on the general biology of this primitive fish (Bigelow and Schroeder, 1953; Crescitelli, 1969).

Little information has been published on the food habits of *H. colliei*. Dean (1906) reported that *Chimaera* (*Hydrolagus*) *colliei* fed on small isospondylous fishes, opisthobranchs, annelids, crustaceans, mollusks, squids, and nudibranchs. Olsson (1896) and Legendre (1944) reported that *Chimaera monstrosa* fed on mollusks, decopods, annelids, amphipods, echinoderms, and coelenterates.

Several studies have been conducted on the parasites of *H. colliei*. Wardle (1932) reported that most ratfish contained a pair of *Gyrocotyle urna* in the anterior region (spiral valve) of the intestine. Lynch (1945) concluded that *G. urna* should be divided into *G. urna* and *G. fimbriata*. Koratha (1960) examined two *H. colliei* from

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Baja California and found two digenea (*Otodistomum* sp.) and one cestode from the intestine, one hirudinean (*Branchellion* sp.) from the skin surface, and three copepods (*Chondracanthus epacthes*) and one monogenea from the gills. A monogenea reported from the gills of ratfish from Washington waters was *Octobathrium leptogaster* (Bonham, 1950). Wilson (1935) reported the copepods *Acanthochondria clavata* and *A. epachthes* from the claspers and gills, respectively, of *H. colliei* from California waters. Kabata (1968) could not accept Wilson's (1935) identification of *A. clavata*, because the species had never been found outside the North Sea, and described *A. holocephalarum* from the claspers of ratfish captured off British Columbia.

Most morphometric studies of ratfish have been descriptive or histological in nature. Sanford, Clegg, and Bonham (1945) studied the liver oil and vitamin A content of 35 ratfish captured off Tatoosh Island, Wash. These factors were related later to size and sex of ratfish by Pidlaoan (1950). Halstead and Bunker (1952) described the venom apparatus and anatomy of the dorsal spine of ratfish. They concluded that the venom of *H. colliei* was not capable of inflicting fatal injuries to man. A histological study of the digestive tract and of the pituitary of *H. colliei* was conducted by Clothier (1957) and Sathyanesan (1965), respectively.

Stanley (1961) performed a morphometric study of the genital systems of *H. colliei* and found that summer was the peak reproductive period although one-third of the females and all of the males evidenced reproductive activity throughout the year. Sexual maturity was attained at 24-25 cm (S-V)[4] for females and 18.5-20 cm (S-V) for males.

METHODS

Four collections totaling 292 ratfish were made by otter trawl off the coast of Oregon at depths ranging from 50 to 120 fm from 1965 to 1967. The collection from off Newport ($N = 189$) was frozen while specimens collected off Cape Blanco ($N = 44$), Cape Arago ($N = 35$), and Astoria ($N = 24$) were preserved in 10% Formalin.

All ratfish were examined as follows: Sex was determined by inspection of the gonads; snout to vent length was measured in millimeters, and total weight was measured in grams; all specimens were examined for internal and external parasites; alimentary canals were examined along their entire length for food items; and dental plates, dorsal spines, left pectoral fins, and a piece of the vertebral column were decalcified, sectioned frozen, treated with Delafield's hematoxylin stain, and examined for growth structures indicative of age. Both eye lenses were removed from specimens in the Newport and Astoria collections. The wet and dry weight of each lens was determined to the nearest ten thousandth of a gram. For wet-weight determinations, lenses were stored in 10% Formalin for 1 month, removed and blotted, and immediately weighed. For dry weight determinations, the lenses were then desiccated at 80°C for 82 hr and reweighed. The 82-hr drying period was determined from a curve of weights of 10 lenses dried at 80°C and weighed at progressive time intervals. The 82-hr period assured evaporation to a stable weight.

Most statistical analyses of body length-body weight and body length-eye-lens weight relationships were performed on a CDC 3300 computer[5] utilizing program FISH 6669 in the Department at Oregon State University.

RESULTS AND DISCUSSION

There was a highly significant correlation ($P = 0.01$) of body length to body weight for male and female ratfish in the large Newport collection and for the aggregate of each sex collected (Table 1). Based on the coefficient of determination (r^2) (Croxton, 1953), more than 87% of the variation in weight in males and more than 96% in females was attributable to the variation in length of the ratfish. The length-

[4] Body length measured from the tip of the snout to the anterior edge of the vent.

[5] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

TABLE 1.—Data to describe length-weight relationship (log weight = log a + b log length) for male and female ratfish collected off Oregon during 1965-67.

Location	Sex	Sample size	Constant log a	Constant b	r	Sign. Level of r (P = 0.01)*	r^2**
Newport	Male	128	—2.0168	2.0447	0.9352	0.234	0.8746
Newport	Female	56	—3.1384	2.5336	.9824	.361	.9651
Total†	Male	175	—4.3217	3.0546	.9917	.210	.9835
Total†	Female	112	—9.1692	2.9720	.9943	.257	.9886

* From Table X in Quenouille (1952).
** Coefficient of determination (Croxton, 1953).
† Composite of collections from Newport, Astoria, Cape Arago, and Cape Blanco.

weight relationship for male and female ratfish collected off Newport is defined and illustrated in Figure 1.

A taxonomic list of all food organisms identified from the alimentary canals of 283 ratfish is presented in Table 2. The table also contains lists of the relative importance of food items by the frequency of occurrence and numerical methods (Lagler, 1956) and gives the locations of the collections in which the food items were found.

Based on these data, ratfish appear to be opportunistic feeders. The most important food items (>10% occurrence) were shrimp (*Pandalus* and *Crago*), mollusks (*Musculus* and *Amphissa*), and echinoderms (*Brisaster*). In general, young and adult ratfish ate the same foods. Dean (1906) found seaweed in the alimentary canals of ratfish, but we did not find any plant materials in the specimens we examined.

In the Cape Arago collection, ratfish were eaten by ratfish. One egg capsule and a caudal fin were eaten by two large females (280 mm). We are not aware of any previous record of cannibalism in ratfish. Of the teleostomi, flatfish appeared to be taken most frequently by ratfish. The two flatfish found were *Hippoglossoides elassodon* and *Esopsetta jordani*.

In the food habits study, we did not use a volumetric method of examination because in many alimentary canals only shells and fragments remained. Also, materials such as carapaces of shrimp have a large surface to volume relationship which causes them to displace little water or to float. Ratfish often void ingested matter between capture and landing, making volumetric measurements inaccurate. Dean (1906) commented on this habit, and we noticed it in ratfish captured by hook and line. In addition, we found *Gyrocotyle* in the mouths of some trawl-caught ratfish, indicating that the contents of the alimentary canals recently had been voided. According to Lynch (1945), *Gyrocotyle* would normally be restricted to the anterior section of the intestine (spiral valve).

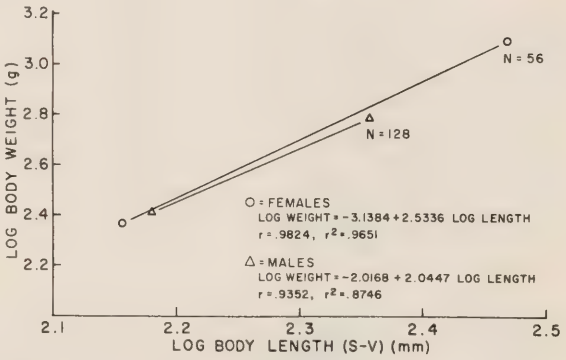

FIGURE 1.—Length-weight relationship of male and female ratfish collected off Newport, Oreg., 1965.

The parasites found on or in the ratfish were *Gyrocotyle urna*, *G. fimbriata*, and the copepod, *Acanthochondria* sp. Table 3 lists the frequency of *Gyrocotyle* occurring in the four collections of ratfish. Both *G. fimbriata* and *G. urna* appeared in about equal numbers in the Newport collection, but only *G. fimbriata* occurred in the Astoria and Cape Arago collections. The frequency of infestation by *Gyrocotyle* in young fish from the Cape Blanco collection was 30%. We did not find evidence of mass infestation by *Gyrocotyle*, as suggested by Wardle (1932). The young fish (<50 mm) contained from zero to two *Gyrocotyle* each. The voiding of canal contents by the ratfish interfered with obtaining an accurate estimation of the degree of infestation.

TABLE 2.—Taxonomic list[1] and relative importance of food organisms identified from the alimentary canals of 283 ratfish (*Hydrolagus colliei*)[2] collected off Oregon during 1965-1967.

Organisms	Frequency of occurrence (%)	Numerical method[3]		Location[4]			
		Organisms	%	A	N	CA	CB
Phylum Annelida							
Class Polychaeta							
Aphrodita	4.4	10	1.0	×	×		×
Unidentified	2.2	10	1.0		×		×
Phylum Mollusca							
Class Gastropoda							
Amphissa	33.4	1,016	74.5	×	×	×	×
Amygdalum	2.2	9	1.0				×
Yoldia	2.6	6	0.0+		×		
Musculus	24.6	66	4.9	×	×	×	×
Leptopecten	0.9	2	0.0+		×		
Pecten	1.8	7	0.0+			×	
Cardiomya	6.1	27	2.0				×
Calliostoma	0.4	1	0.0+				×
Searlesia	0.4	1	0.0+	×			
Class Scaphopoda							
Dentalium	3.1	7	0.0+		×		×
Phylum Arthropoda							
Class Crustacea							
Livoneca	4.8	26	2.0		×	×	×
Crago	12.3	32	2.3		×		
Pandalus	20.2	81	5.9	×		×	×
Cancer	0.9	2	0.0+	×	×		
Chionectes	0.4	1	0.0+				×
Unidentified	3.5	13	1.0		×		
Phylum Echinodermata							
Class Echinoidea							
Brisaster	11.0	25	1.8	×	×	×	
Strongylocentrotus	0.9	2	0.0+	×		×	
Phylum Chordata							
Class Chondrichthes							
Hydrolagus	0.9	2	0.0+			×	
Class Osteichthyes							
Pleuronectidae	0.7	2	0.0+		×	×	
Unidentified	5.5	13	1.0	×	×	×	
Unknown	0.4	1	0.0+		×		
Total		1,362	98.4+				

[1] After Smith et al. (1954), Barnes (1963), and Bailey (1970).
[2] Of the 283 ratfish, 224 contained food organisms.
[3] Fragments (less than one-half an animal) were recorded as one individual.
[4] Locations were: A = Astoria, N = Newport, CA = Cape Arago, and CB = Cape Blanco.

Gyrocotyle were found lodged in the folds of the spiral valve and were not embedded in the intestinal wall, thus making expulsion by violent intestinal movements possible.

In the Cape Arago collection, 7 of the 21 adult male ratfish had from two to eight *Acanthochondria* sp. attached to the free ends of their claspers. The immature males and the females did not carry this copepod. The species is similar to, but not the same as, *A. compacta.*[6]

An unidentified fungus, which occurred on the intestine of 29% of the Newport collection, was not necessarily a parasite as it may have developed in the interval between capture and preservation. No visible lesions or other damage were noticed on the body or alimentary canal surfaces of the ratfish in which the fungus occurred. The fungus appeared to be of nonseptate, white, filamentous type.

Sex and relative age of ratfish can be determined by examination of the secondary sex characteristics. Males possess a frontal tenaculum, prepelvic tenacula, and claspers, whereas fe-

[6] Personal communication, Dr. Satyu Yamaguti, Beltsville, Md., June 13, 1967.

TABLE 3.—*Gyrocotyle* found in 283 ratfish (*Hydrolagus colliei*) collected off the coast of Oregon, 1965-1967.

Location	Total number of *Gyrocotyle*[1]			Number of ratfish examined	Percent infested[2]
	G. fimbriata	*G. urna*	Unidentified		
Newport	50(34)	62(39)	38(25)	184	53.2(60.0)
Astoria	8(7)	-- --	-- --	24	29.2(31.8)
Cape Arago	40(23)	-- --	-- --	35	65.8(79.4)
Cape Blanco	18(11)	4(2)	-- --	40	30.0(35.4)

[1] Number in parenthesis is the number of ratfish infested.
[2] Number in parenthesis is the percent infestation when alimentary canals that contained neither food nor parasites were excluded.

males do not possess these structures but develop paired oviducal openings not possessed by males. Development of these structures can be used to separate ratfish into young, immature, and adult age groups. Young males have a frontal tenaculum streak and diminutive claspers (Figure 2); immature males have a small frontal tenaculum and claspers which are not perforated at their free ends (Figure 3); and mature males have a well-developed frontal tenaculum and well-developed claspers which are perforated at their free ends (Figure 4). Young females have no oviducal openings (Figure 2); the oviducts of immature females have small openings (Figure 3); and mature females have oviductal openings which are large, elongated, and swollen

FIGURE 2.—Regions of young ratfish showing (A) the frontal tenaculum streak, and (B) the small claspers of the male; and (C) the absence of a frontal tenaculum streak, and (D) the absence of oviductal openings in the female.

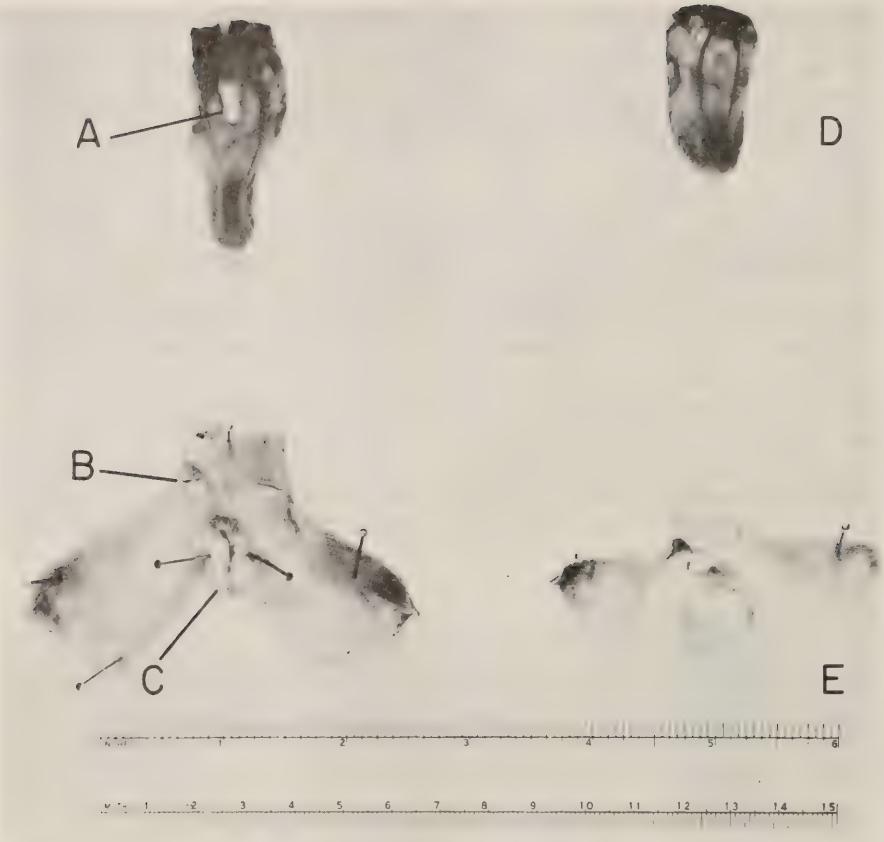

FIGURE 3.—Regions of immature ratfish showing (A) the frontal tenaculum, (B) the prepelvic tenacula, and (C) the claspers of the male; and (D) the absence of a frontal tenaculum, and (E) the presence of small openings to the oviducts of the female.

(Figure 4). Attempts to age ratfish on the basis of length-frequency distributions were inconclusive.

When dry eye-lens weight was compared to body length for specimens in the Newport collection, lens weight was positively correlated with increasing body length for males (N = 128), but was not correlated with body length for females (N = 56) (Figure 5). There was no difference in the dry weights of the right and left eye lens at the 95% level of confidence. Wet eye-lens weights were similarly related to body lengths with the coefficient of determination (r^2) for males being 0.8788 and 0.9292 for the right and left eye lens respectively, and for females being 0.0017 and 0.0133 for the right and left eye lens respectively.

We can offer no logical explanation for the lack of positive correlation between eye-lens weight and body length for female ratfish. Data for males and females were processed simultaneously and were consistent, by sex, for left and right and for wet and dry eye-lens weights. Because all but eight females exceeded 230 mm in length, most eye-lens growth may take place between birth (30-40 mm [Stanley, 1961]) and maturity (240-250 mm [Stanley, 1961]). The possibility of decreasing density of the lens with size (and maturity) should be investigated.

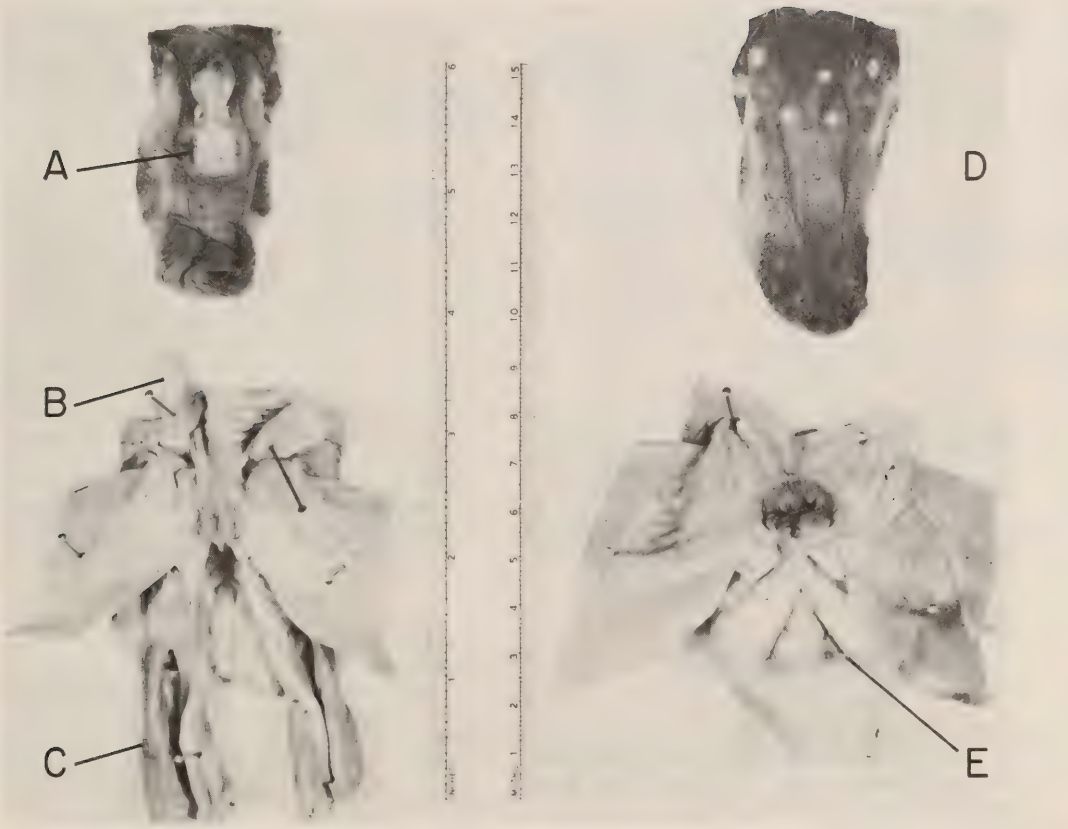

FIGURE 4.—Regions of mature ratfish showing (A) the frontal tenaculum, (B) the prepelvic tenacula, and (C) the claspers of the male; and (D) the absence of a frontal tenaculum, and (E) the presence of well-developed openings to the oviducts of the female.

In general, there was an increase in the size of other body parts (teeth, vertebrae, base of left pectoral fin, and base of dorsal spine) with increasing body length. We did not find any layering or structures in these body parts which were sufficiently correlated with body length to provide a possible means of age determination.

The number of tritors (horizontal ridges) on the posterior side of the left vomerine dental plate was compared to the respective body length of male and female ratfish in the Cape Blanco and Newport collections. In general, the number of tritors increased with increasing body length (Figure 6). Two problems arose in using this structure as a basis for age determination: (1) No comparison to known-aged fish was possible. (2) The amount of wear on these ridges per unit of time was not known.

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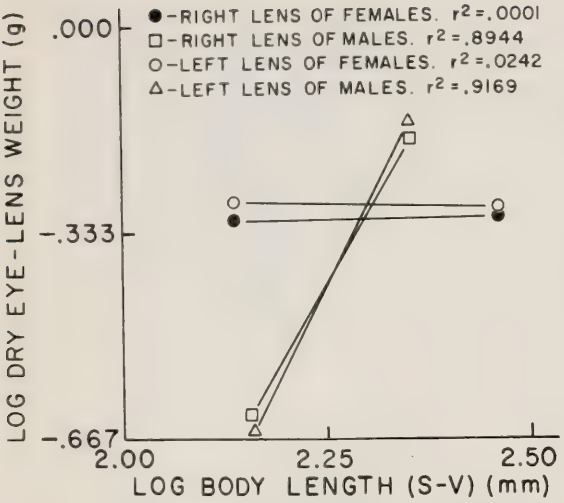

FIGURE 5.—Log dry eye-lens weight compared to log body length for ratfish collected off Newport, Oreg., 1965.

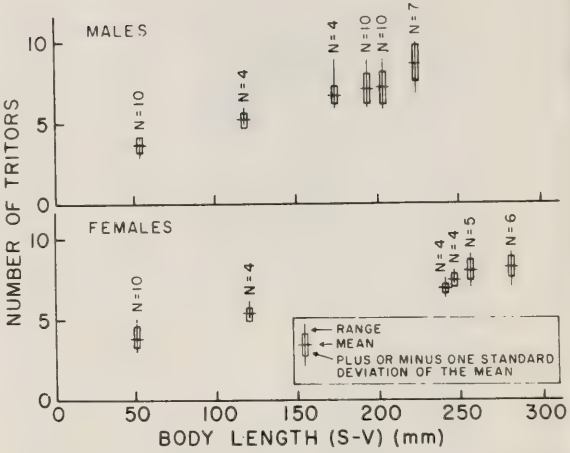

FIGURE 6.—Comparison of the number of tritors on the posterior side of the vomerine dental plate to body length of ratfish collected off Oregon, 1965-1967.

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OCEAN DISTRIBUTION, GROWTH, AND EFFECTS OF THE TROLL FISHERY ON YIELD OF FALL CHINOOK SALMON FROM COLUMBIA RIVER HATCHERIES

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ABSTRACT

Data are presented depicting the distribution of some stocks of Columbia River hatchery fall chinook salmon in the northeast Pacific Ocean. These are based on recoveries of marked fish. Also presented are the apparent growth histories for fish from the Kalama and Spring Creek Hatcheries as well as a graphic population model for Columbia River fall chinook salmon. Finally, the effect on total yield for varying troll fishing mortalities for the 3-, 4-, and 5-year-old fish is analyzed and the results depicted in three-dimensional yield diagrams. In most instances, at least at the lower levels of estimated natural mortality, troll fishing of the younger fish reduced total yield.

A cooperative program was undertaken between the various fishery agencies in the United States and Canada to estimate the contributions to various fisheries of fall chinook salmon (*Oncorhynchus tshawytscha*) produced by a number of Columbia River hatcheries. Approximately 10% of the output from 12 hatcheries for the brood years 1961-64 was marked by the removal of certain fins. The design of this experiment, including a detailed account of the procedures used in calculating the number of marked fish recovered, and details of mark recoveries for the 1961 brood have been reported by Worlund, Wahle, and Zimmer (1969). Details of mark recoveries for the 1962 and 1963 broods were given by Rose and Arp (1970)[2] and by Arp et al. (1970[3], respectively. Cleaver (1969) made a detailed analysis of the 1961 brood based on mark recoveries. His analysis included estimating ocean mortality rates, maturity schedules, and, for the Spring Creek and Kalama fish, the effect of no ocean fishing on total yield. Henry (1971) made a similar analysis for the 1962 brood and, wherever possible, compared the results with those obtained for the 1961 brood. The general release and recovery areas covered by this marking program are shown in Figure 1.

Although a total of 12 hatcheries was involved in this study, fish from only two hatcheries, Spring Creek and Kalama, received specific identifying marks for all 4 years. Each year fish from two of the other ten participating hatcheries (but two different ones each year) also received special identifying marks. In addition to specific marks for four hatcheries each year, a certain proportion of the output from all participating hatcheries had a common mark. This mark — that is a composite of all the hatcheries — is referred to as the general mark. Thus, it is possible for only Spring Creek, Kalama, and general mark fish to analyze mark recoveries from all four brood years.

In the report, I have analyzed the mark recoveries for Spring Creek, Kalama River, and general marked Columbia River hatchery fall chinook salmon from the four consecutive brood

[1] National Marine Fisheries Service Northwest Fisheries Center, 2725 Montlake Boulevard East, Seattle, WA 98102.

[2] Rose, J. H., and A. H. Arp. 1970. Contribution of Columbia River hatcheries to harvest of 1962 brood fall chinook salmon (*Oncorhynchus tshawytscha*). Bur. Commer. Fish., Columbia Fish. Program Off., Appraisal Section, Portland, Oreg. 27 p. (processed).

[3] Arp, A. H., J. H. Rose, and S. K. Olhausen. 1970. Contribution of Columbia River hatcheries to harvest of 1962 brood fall chinook salmon (*Oncorhynchus tshawytscha*). U.S. Dep. Commer., Natl. Oceanic Atmos. Admin., Natl. Mar. Fish. Serv., Columbia Fish. Program Off., Portland, Oreg., Econ. Feasibility Rep. 1. 33 p. (processed).

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FISHERY BULLETIN: VOL. 70. NO. 2, 1972.

FIGURE 1.—Sampling areas in marine fisheries and release locations (inset) for the Columbia River hatchery evaluation program (from Lander, 1970).

years (1961, 1962, 1963, and 1964). I have demonstrated some of the differences in ocean distribution, contributions to various fisheries, and growth that occur between hatcheries—even within hatcheries—for different brood years. I also have presented a graphic population model for Columbia River fall chinook salmon. This model depicts all the factors affecting these stocks of salmon throughout their life history. Finally, within the general framework of the mortality estimates developed for the 1961 brood (Cleaver, 1969) and 1962 brood (Henry, 1971), I have analyzed the portion of the population model pertaining to the commercial fisheries to determine the overall effect on total yield for varying levels of ocean troll fishing mortalities on the 3-, 4-, and 5-year old fish.

RECOVERIES BY AREA

The ocean distribution of mark recoveries and contributions to the various fisheries was quite different for Kalama, Spring Creek, and general marked fish. Pulford (1970) listed the contribution of Columbia river hatchery fall chinook (all hatcheries combined) to the various fisheries along the Pacific Coast for 1966 only. Lander (1970) analyzed the distribution along the coast and contribution to the various fisheries in considerable detail for each hatchery; his data included sampling through 1966 only. In Table 1 are listed the calculated total recoveries by geographical area for the 1961 through 1964 brood years of special marked Kalama and Spring Creek fall chinook salmon and general marked

TABLE 1.—Calculated total recoveries, by age of fish and type of mark, for fall chinook salmon of the 1961-64 broods that were marked and released at Columbia River hatcheries.

Brood and area	Spring Creek mark age (years)					Kalama mark age (years)					General mark age (years)				
	2	3	4	5	Total	2	3	4	5	Total	2	3	4	5	Total
1961															
Alaska	*	0	0	0	0	*	5	35	4	44	*	0	7	0	7
Brit. Col.	*	841	164	5	1,010	*	441	480	91	1,012	*	4,106	1,871	218	6,195
Wash. Com.	4	1,084	82	0	1,170	0	149	142	7	298	0	3,241	455	41	3,737
Wash. Sport	152	431	97	0	680	21	78	100	9	208	375	1,681	416	67	2,539
Oreg. Ocean	4	130	24	0	158	0	21	4	0	25	0	396	36	0	432
Col. River	22	518	685	17	1,242	0	38	399	111	548	72	2,158	3,544	176	5,950
Calif.	*	25	0	0	25	*	2	0	0	2	*	23	0	6	29
Total	182	3,029	1,052	22	4,285	21	734	1,160	222	2,137	447	11,605	6,329	508	18,889
1962															
Alaska	0	0	0	0	0	0	0	4	0	4	0	0	5	2	7
Brit. Col.	0	75	90	9	174	0	162	155	23	340	51	1,183	802	48	2,084
Wash. Com.	0	150	33	5	188	0	47	15	0	62	8	973	130	4	1,115
Wash. Sport	34	140	24	0	198	0	76	7	8	91	163	540	108	27	838
Oreg. Ocean	0	11	3	0	14	0	8	4	0	12	2	37	3	0	42
Col. River	10	272	85	0	367	6	21	60	10	97	50	1,216	606	24	1,896
Calif.	0	0	0	0	0	0	0	0	0	0	0	6	0	0	6
Total	44	648	235	14	941	6	314	245	41	606	274	3,955	1,654	105	5,988
1963															
Alaska	0	0	0	0	0	0	5	14	0	19	0	0	9	*	9
Brit. Col.	23	557	224	6	810	0	233	195	45	473	55	4,464	2,246	201	6,966
Wash. Com.	0	381	38	0	419	0	107	71	5	183	5	3,227	464	10	3,706
Wash. Sport	120	329	103	0	552	138	139	53	12	342	1,189	2,569	451	46	4,255
Oreg. Ocean	0	63	10	0	73	2	27	13	0	42	4	652	165	3	824
Col. River	29	164	275	15	483	7	32	44	47	130	121	1,182	2,418	317	4,038
Calif.	0	4	0	0	4	0	0	0	0	0	0	12	12	15	39
Total	172	1,498	650	21	2,341	147	543	390	109	1,189	1,374	12,106	5,765	592	19,837
1964															
Alaska	0	0	*	*	0	0	0	*	*	0	0	0	*	*	0
Brit. Col.	7	589	432	16	1,044	0	45	478	64	587	10	1,339	1,446	92	2,887
Wash. Com.	0	906	127	0	1,033	0	65	37	5	107	4	2,268	354	3	2,181
Wash. Sport	244	581	70	10	905	38	44	26	0	108	483	1,506	249	0	2,212
Oreg. Ocean	127	171	27	0	325	0	10	13	0	23	151	614	170	0	935
Col. River	15	447	504	24	990	0	3	58	56	117	19	1,001	1,204	169	2,393
Calif.	0	8	2	0	10	0	0	0	0	9	0	0	1	0	1
Total	393	2,702	1,162	50	4,307	38	176	612	125	951	667	6,728	3,424	266	11,085

* No sampling.

Columbia River fall chinook salmon. No single fin marks are included. These same data are depicted in Figures 2-4 for calculated numbers of marked fish recovered and in Figures 5-7 as percentages of the total number of marks recovered by each age group within each brood year.

More Spring Creek mark recoveries (Figure 2) were recovered as age 3 fish than at any other age. Both the age 2 and age 3 recoveries came principally from Washington State fisheries, whereas most of the age 4 and age 5 recoveries were from the British Columbia troll fishery and the Columbia River gillnet fishery. For all ages combined, Washington State fisheries had the most recoveries of Spring Creek fish with about equal numbers recovered in the British Columbia and Columbia River fisheries. From 18 to 35% of the total recoveries were made in British Columbia fisheries (Figure 5). No Spring Creek fish were recovered from the Alaska fisheries.

The recoveries of marked Kalama fish were distributed somewhat differently than marked Spring Creek fish (Figure 3). Although recoveries of marked 2-year-old fish occurred primarily in the Washington sport fishery, 3- and 4-year-old recoveries and the recoveries for all ages combined came principally from the British Columbia troll fishery. Most of the recoveries occurred with the 3- and 4-year-old fish. British Columbia fisheries had from 40% to 60% of the total recoveries (Figure 6), a considerably higher percentage than for Spring Creek fish. There were very few recoveries from the Alaska fisheries.

General mark recoveries seemed to be more similar to Spring Creek recoveries than to Kalama recoveries, indicating that most of the fish from the participating hatcheries had an ocean distribution and maturity schedule more like Spring Creek fish than Kalama fish. For the general mark recoveries, the 2-year-old recoveries were mainly from the Washington sport fishery (Figure 4). The Washington fisheries accounted for 38-53% of the 3-year-old mark recoveries, whereas both the 4- and 5-year-old recoveries came mainly from the British Columbia troll fishery and the Columbia River gill-

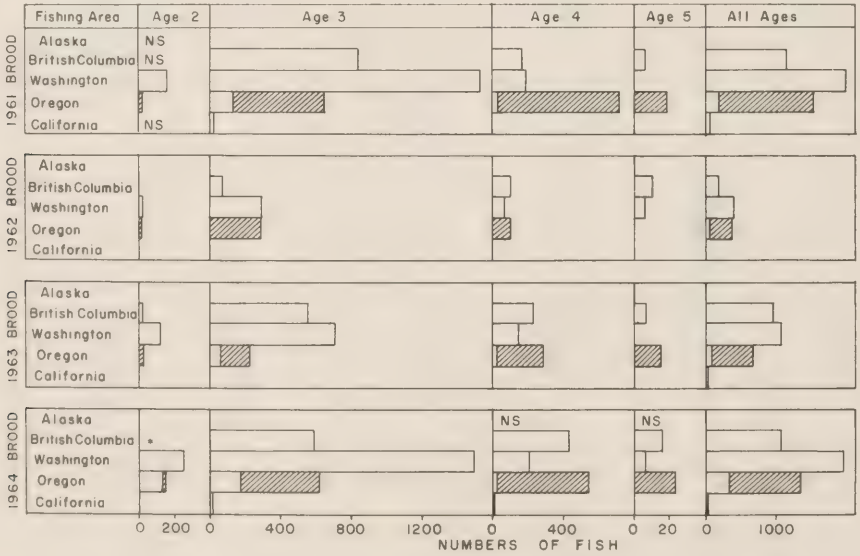

FIGURE 2.—Calculated total recoveries (in numbers of fish) of special marked Spring Creek hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 10 recoveries.

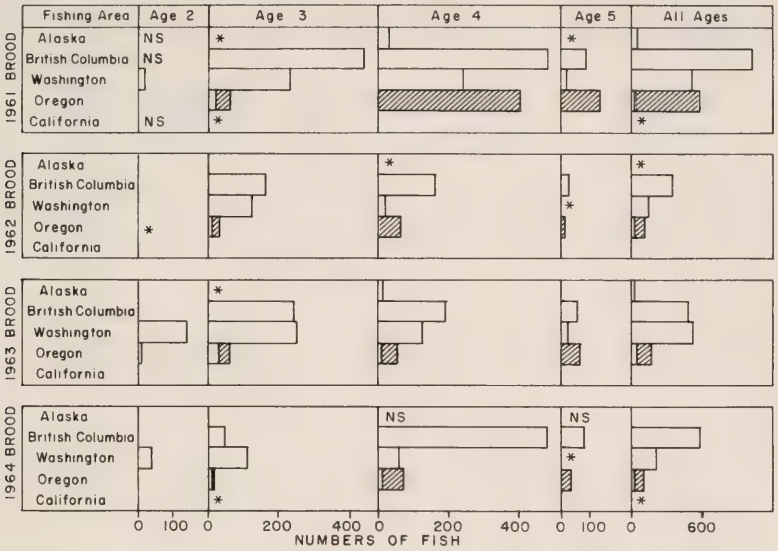

FIGURE 3.—Calculated total recoveries (in numbers of fish) of special marked Kalama hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 10 recoveries.

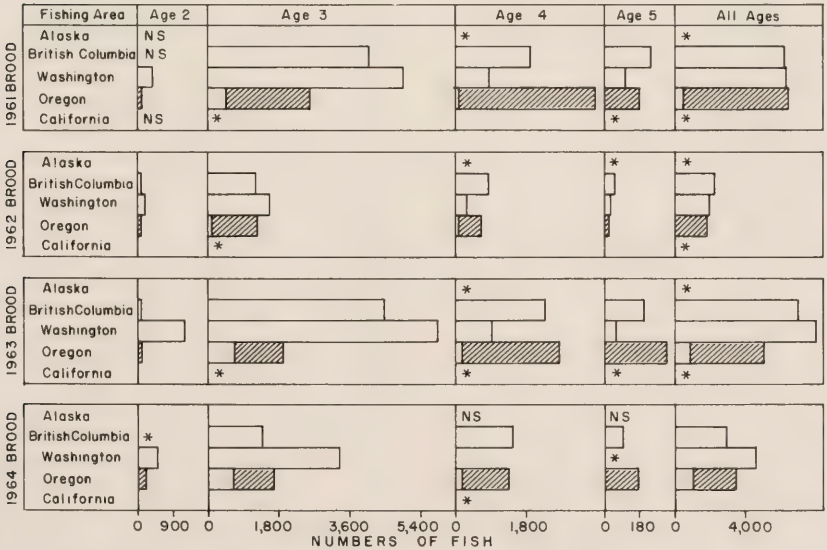

FIGURE 4.—Calculated total recoveries (in numbers of fish) of general marked Columbia River hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 50 recoveries.

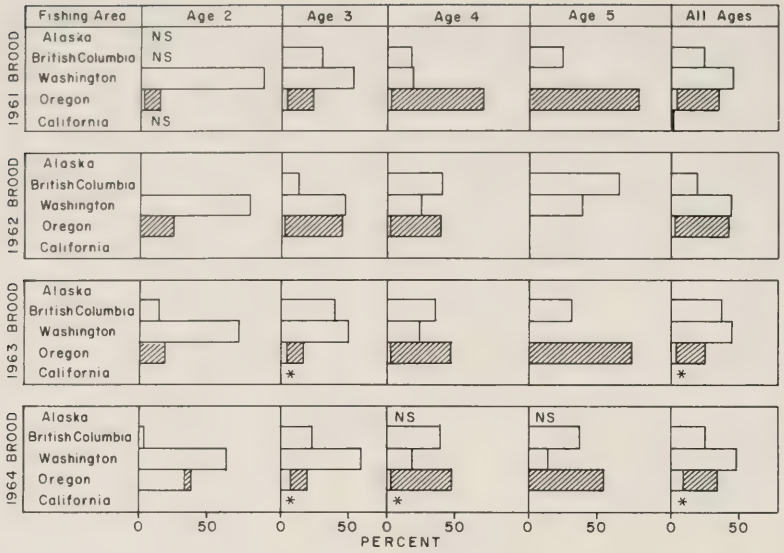

FIGURE 5.—Calculated total recoveries (in percent) of special marked Spring Creek hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 1 percent.

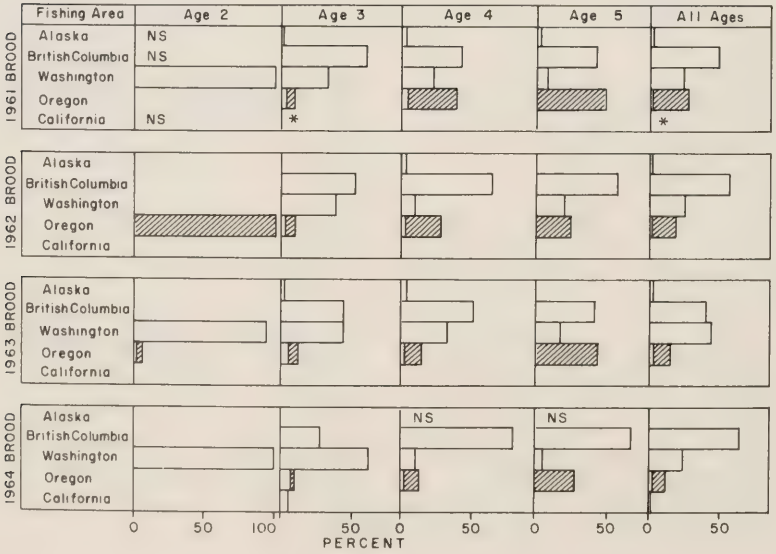

FIGURE 6.—Calculated total recoveries (in percent) of special marked Kalama hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 1 percent.

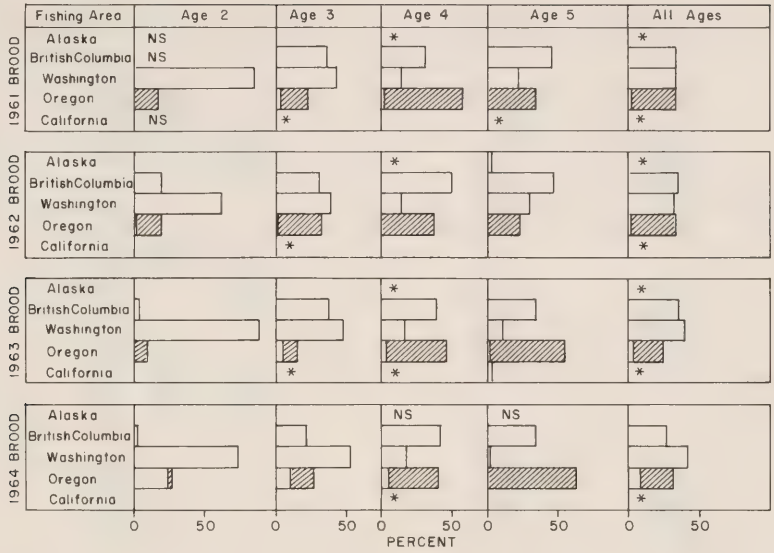

FIGURE 7.—Calculated total recoveries (in percent) of general marked Columbia River hatchery fall chinook salmon, by age, in different fishing areas, 1961-64 brood years (Columbia River recoveries are shown as the shaded portion of the Oregon recoveries). NS = no sample; * = less than 1 percent.

net fishery (Figure 7). For all ages combined, the recoveries were fairly equally distributed between the British Columbia, Washington, and Columbia River fisheries.

As mentioned above, the age at recovery for Kalama fall chinook salmon was somewhat different than the age at recovery of the other two groups of marked fish. This is more clearly seen in Figure 8 where the calculated total ocean recovery of special marked Spring Creek, Kalama, and general marked fish (by age) for these four brood years is shown. Thus, for Spring Creek most of the ocean recoveries were as 3-year-old fish (66-83%); Kalama mainly as 3- (21-57%) and 4-year-olds (32-66%); and general marks mainly as 3-year-olds (64-73%).

SIZE AND GROWTH

Not only were the recoveries by age and area different for Spring Creek and Kalama fall chinooks, but these fish also experienced different apparent growth patterns. In Figure 9 are shown the average weights, by age and sex, of marked Spring Creek and Kalama fish recovered in the Columbia River gillnet fishery. The Kalama fall chinooks were generally smaller than the Spring Creek fish at ages 2-4, whereas the Kalama fish were larger at age 5. This change in the relative size of fish from these two stocks of salmon might reflect the selective effects of a more intensive troll fishery on the faster growing, earlier maturing Spring Creek fish, whereby the larger Spring Creek fish are more apt to be caught by the troll fishery at ages 2 and 3. Since data are limited for some of the sex-age categories, I have combined the data for all brood years and both sexes and have completed a von Bertalanffy type growth equation for these two stocks (Figure 10). The relatively faster growth at the younger ages and the more abrupt slowing down of growth at the older age is evident for the Spring Creek fish. Parameters calculated for Spring Creek were: $W_\infty = 12.76$ kg, $t_0 = 1.02$, and $k = 1.1$; for Kalama they were: $W_\infty = 18.44$ kg, $t_0 = 0.77$, and $k = 0.6$. These growth parameters clearly detail the growth differences between these two stocks and would be useful in any future dynamic pool type of analysis (Beverton and Holt, 1957) of potential production from them.

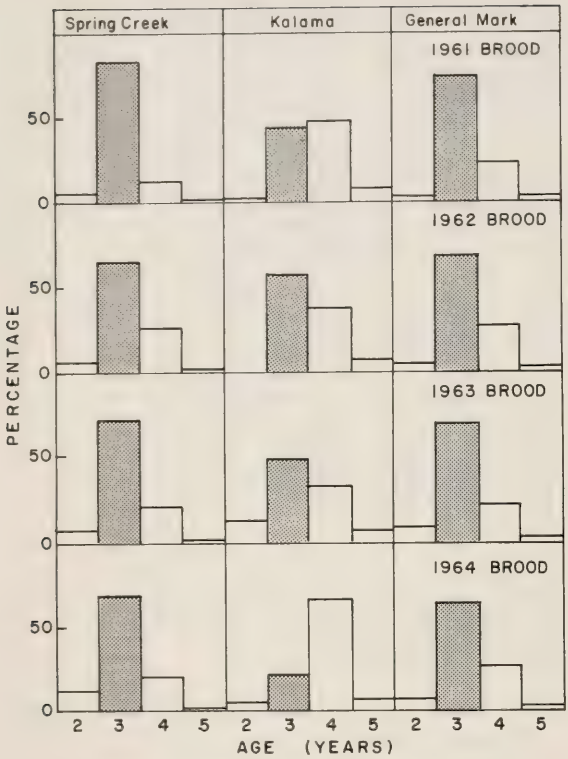

FIGURE 8.—Calculated total ocean recoveries (in percent), by age, of special marked Spring Creek, Kalama, and general marked Columbia River hatchery fall chinook salmon, 1961-64 brood years.

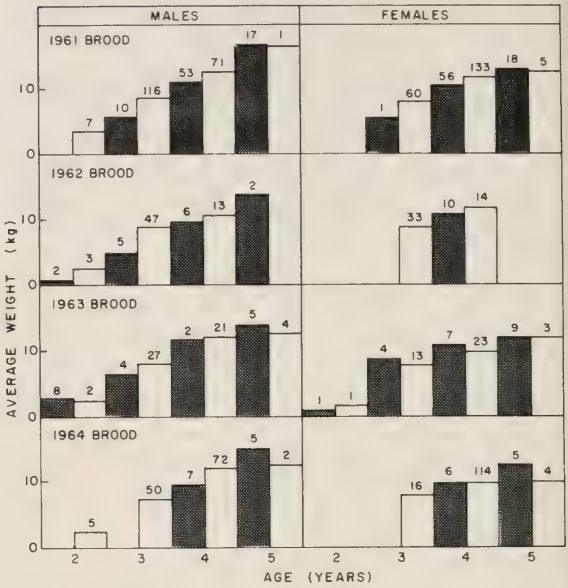

FIGURE 9.—Average weight (kilograms) by age and sex, of 1961-64 brood Spring Creek and Kalama special marked hatchery fall chinook salmon caught in the Columbia River gillnet fishery. Shaded columns represent data for Kalama salmon — clear columns, Spring Creek. Numbers indicate sample size.

GRAPHIC POPULATION MODEL FOR COLUMBIA RIVER FALL CHINOOK

To more clearly understand all the forces affecting a stock of fish, it often is convenient to depict the population in a simulated flow chart or block diagram. Shapiro and Andreev (1969) show such a diagram for chum salmon (*O. keta*). With some modification, their diagram also would be applicable to Columbia River fall chinook salmon as shown in Figure 11. This diagram is based on the following stock characteristics. There are five age groups, four of which are capable of entering the spawning groups, and each brood year diminishes in numbers as a result of natural mortality (M_i) and ocean fishing mortality (F_i). Ocean fishing mortality occurs only on the 2+, 3+, and 4+-year-old-fish. Growth and fecundity differ for each age group, and entry into the spawning part of the population is affected by a probability (P_i). The spawning group is diminished by a river fishing mortality (RF_i). After river fishing mortality, some portion of the spawning fish (k_i) are removed for artificial propagation. Survivals to recruitment resulting from artificial and natural reproduction are taken to be different. The number of recruits (R) is dependent on a survival relationship for the effective fecundity, i.e., R/E.

EFFECT OF TROLL FISHING ON YIELD

A complete analysis of the Columbia River fall chinook population, as depicted in Figure 11, is beyond the scope of this paper. However, I

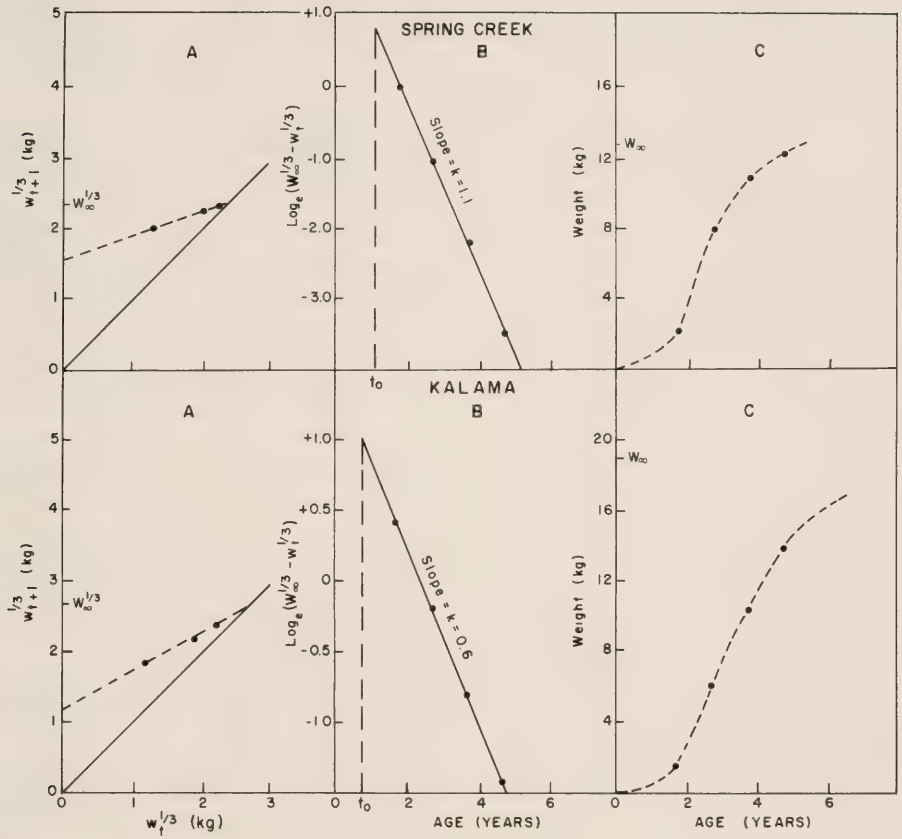

Figure 10.—Successive stages of fitting Spring Creek and Kalama Hatchery fall chinook salmon weight data from Figure 8 to the von Bertalanffy growth equation. Part A shows the relation between average weight at age t and age $t + 1$ — point on the dotted line where $w_t^{1/3} = w^{1/3}{}_{t+1}$ is an estimate of $W_\infty{}^{1/3}$. Part B shows the relation between age and a logarithmic function of the weight used to estimate the value of k (i.e., the slope). Part C shows the calculated growth curve based on the values computed from Parts A and B.

want to analyze a part of the model, the part dealing with the ocean and river fisheries, to show the calculated effect the troll fishery has on total yield for a particular brood year. In these analyses, I have used data developed for the 1961 and 1962 brood years for the Spring Creek and Kalama fall chinooks, based on studies by Cleaver (1969) and Henry (1971), respectively. Where there were some data missing for the 1962 brood Spring Creek fish, I used 1961 data. The starting point for the analyses is at age 1+ in Figure 11.

It is apparent from Figure 11 that given F_i, M_i, P_i, and RF_i, as well as data on average weights of fish at each age, total yields from the ocean and river fisheries for a given number of recruits (R) can be calculated. Henry (1971) gives estimates of F_i and P_i for various values of M_i as well as values for RF_i for 1961 brood Spring Creek and Kalama fish and 1962 brood Kalama fish. Lack of river recoveries of 5-year-old fish prevented estimates of these values for 1962 brood Spring Creek chinook salmon. Henry also lists average weight data, by age, for both

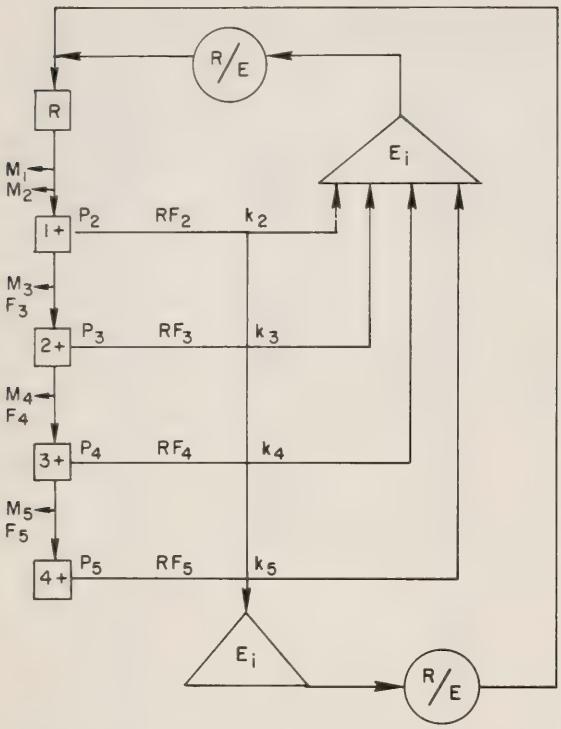

FIGURE 11.—Block diagram of a population model for Columbia River fall chinook salmon (adapted from Shapiro and Andreev, 1969).

M_i = natural mortality rate.
F_i = ocean fishing mortality rate.
RF_i = river fishing mortality rate.
P_i = probability of being a spawner.
k_i = percentage of spawners taken for artificial reproduction.
E_i = effective fecundity/1,000 eggs.
R = number of recruits.
1+, 2+, 3+, 4+ = age of fish.

the ocean and river recoveries of these two stocks of fish.

The procedures followed in these analyses were: given a certain number of recruits (1,000) and a certain M_i (natural mortality) value, and assuming $M_2 = M_3 = M_4$, I calculated the total yield for all ages (numbers caught × average weight) from both the ocean and river fisheries using the P_i values (where P_i is the proportion of the ocean population entering the river to spawn) for the M_i as given by Henry (1971). I let the P_i and RF_i values (where RF_i is the river fishing mortality) remain constant but varied the F_i's (where F_i is the ocean fishing mortality) from 0 to 1.8. This procedure resulted in a 3-dimensional yield diagram (i.e., F_3, F_4, and F_5). The computations were done on an IBM 1130[4] computer and I wrote the program so the computed yields were plotted directly in even yield planes by a CalComp plotter.

Regardless of the natural mortality rate assumed for these computations, it appears that total yields under actual conditions were below the potential yields for both Spring Creek and Kalama fall chinook. In Figure 12 are depicted the calculated maximum potential yields for various values of natural mortality (M_i) and the ocean fishing values (F_i) needed to achieve these maximum yields as well as the calculated yields based on estimated fishing mortality rates for various values of M as given by Henry (1971). It is only with the higher levels of natural mortality (>0.60) or with the 1962 brood Spring Creek fish that a troll fishery on the 3-year-olds (F_3) would have increased yield. At all levels of natural mortality shown, maximum yield required maximum troll fishing effort on the 5-year-old fish (F_5).

The calculated total yield varied considerably depending on the F and M values used. The 3-dimensional outputs for $M = 0.24$ and $F_i = 0$ to 1.8 for the two hatcheries for the 1961 brood year are shown in Figures 13 and 14. I have included a yield diagram for each stock to show the differences in yield that can be generated in this type of analysis as well as to emphasize the differences between these two groups of salmon. The calculated yield planes shown in these figures are actually planes of equal yield passing through the block diagrams. Each yield plane shown consists of points that represent all possible combinations of ocean fishing mortality (F_3, F_4, and F_5)—such that total yield will equal the value shown. In Figure 13, for 1961 brood Spring Creek fish ($M = 0.24$), the maximum yield is at point A ($F_3 = 0$, $F_4 = 0$, and $F_5 = 1.8$) and is slightly over 6,300, the same value as shown in Figure 12. Yield diagrams calculated for $M = 0.96$ were similar to

[4] Use of trade names does not imply endorsement by the National Marine Fisheries Service.

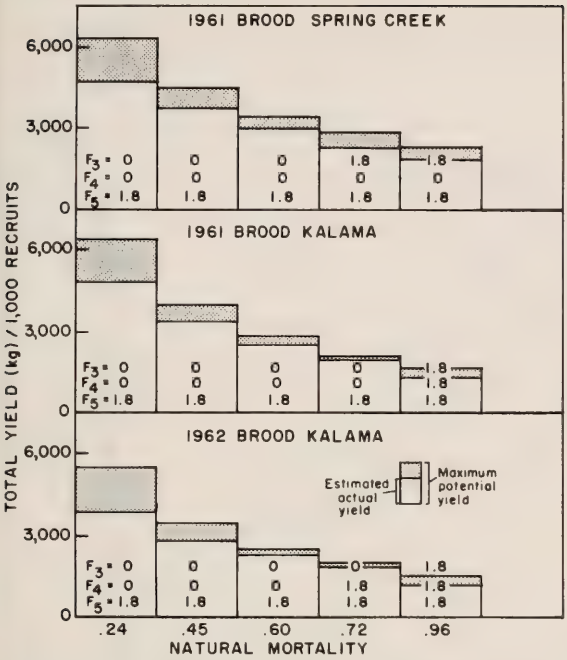

FIGURE 12.—Calculated maximum potential yields (kilograms) per 1,000 recruits for the 1961 brood Spring Creek and Kalama and the 1962 brood Kalama hatchery fall chinook salmon compared with yields calculated for estimated rates of actual ocean fishing mortality (F values shown are those producing maximum potential yields).

those shown except that they depicted lower yields, as would be expected with a higher natural mortality. Similar analyses also were made from the 1962 brood data, but those yield diagrams are not depicted.

In a similar manner to that shown for obtaining the maximum yield, the calculated total yield for any combination of F_3, F_4, and F_5 could be estimated from these graphs. However, the purpose of these graphs is not to estimate single yield values but rather to show the overall effect on yield of varying values of F_3, F_4, and F_5. Thus, Figure 13 shows that the total yields diminish as F_3 and F_4 increase but that F_5 has little effect on total yield. Under these conditions, any troll fishing on 3- and 4-year-old fish would reduce the total yield.

It might be well to re-emphasize that these calculations are based on the assumption of a constant M for the period analyzed. Variations in M during this period would, of course, affect the calculated total yield depending on when the variations occurred and their magnitude. However, a differential M before entry into the troll fishery, i.e., at age 2 and younger, would not affect this analysis.

There is considerable variation in the two yield diagrams, and the reader will have to examine each figure to see in detail the effect of varying levels of troll fishing for that particular brood and level of natural mortality. In general, at the lower levels of natural mortality ($M = 0.24$), increased troll fishing on the younger age group (2+ and 3+) results in reduced yields, whereas the reverse of this generally occurs at the higher level of natural mortality ($M = 0.96$). In other words, at the younger ages and the lower natural mortalities it appears that the rate of growth exceeds the loss due to natural mortality and, consequently, yield is increased by letting the salmon reach an older age before harvesting them. It should be pointed out that even if no fish had been caught in the ocean, the number returning to the river would have been less than the sum of river entry and ocean catch since some of the fish caught in the ocean fishery would have died from natural causes.

The values of M and F that I used, although arbitrary, are believed to cover the range of realistic possible values. Obviously, any values of M could be inserted into the program, but it was felt that $M = 0.24$ and $M = 0.96$ would depict extremes. Also, F_i values greater than 1.8 could be used, but I arbitrarily limited them at this upper boundary because F values of 1.8 considerably exceed any of the F values calculated for either the 1961 or 1962 brood data (Henry, 1971).

The calculated total yields for 1961 and 1962 brood Spring Creek and Kalama fall chinook salmon for various values of natural mortality —if troll fishing could be restricted to only one age group; i.e., troll fishing on only the 3-, 4-, or 5-year-old fish—are shown in Figures 15 and 16. The values for river fishing intensity and proportion spawning are the same as used in the previous analyses. The yields shown are the

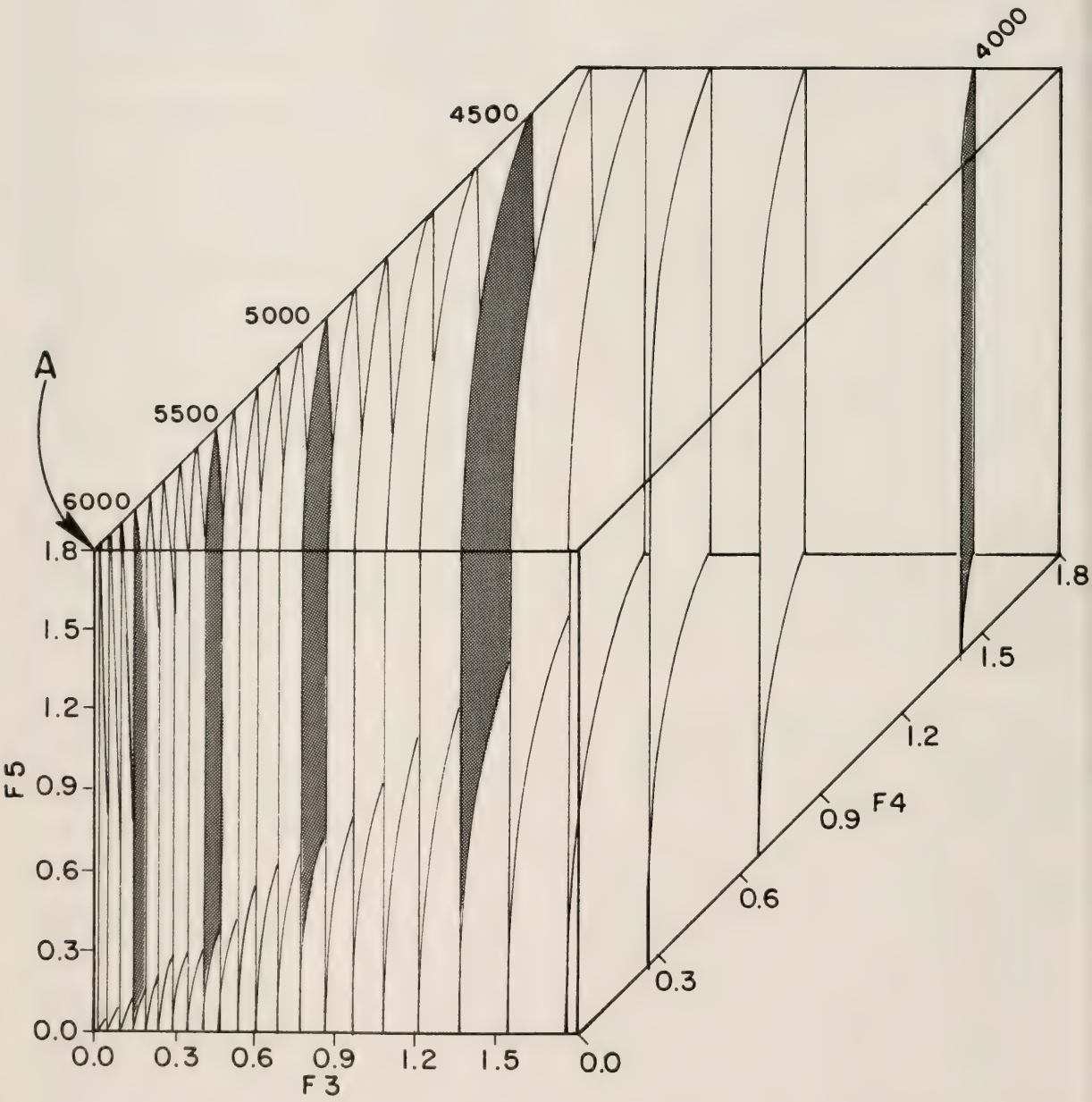

FIGURE 13.—Calculated total yield diagrams (in kilograms per 1,000 recruits) for the 1961 brood Spring Creek hatchery fall chinook salmon with constant natural mortality ($M = 0.24$), varying ocean troll fishing mortality rates (F_3, F_4, and F_5), and the proportion spawning and river fishing intensity remaining constant. Yields are shown by 100-kilogram plane intervals.

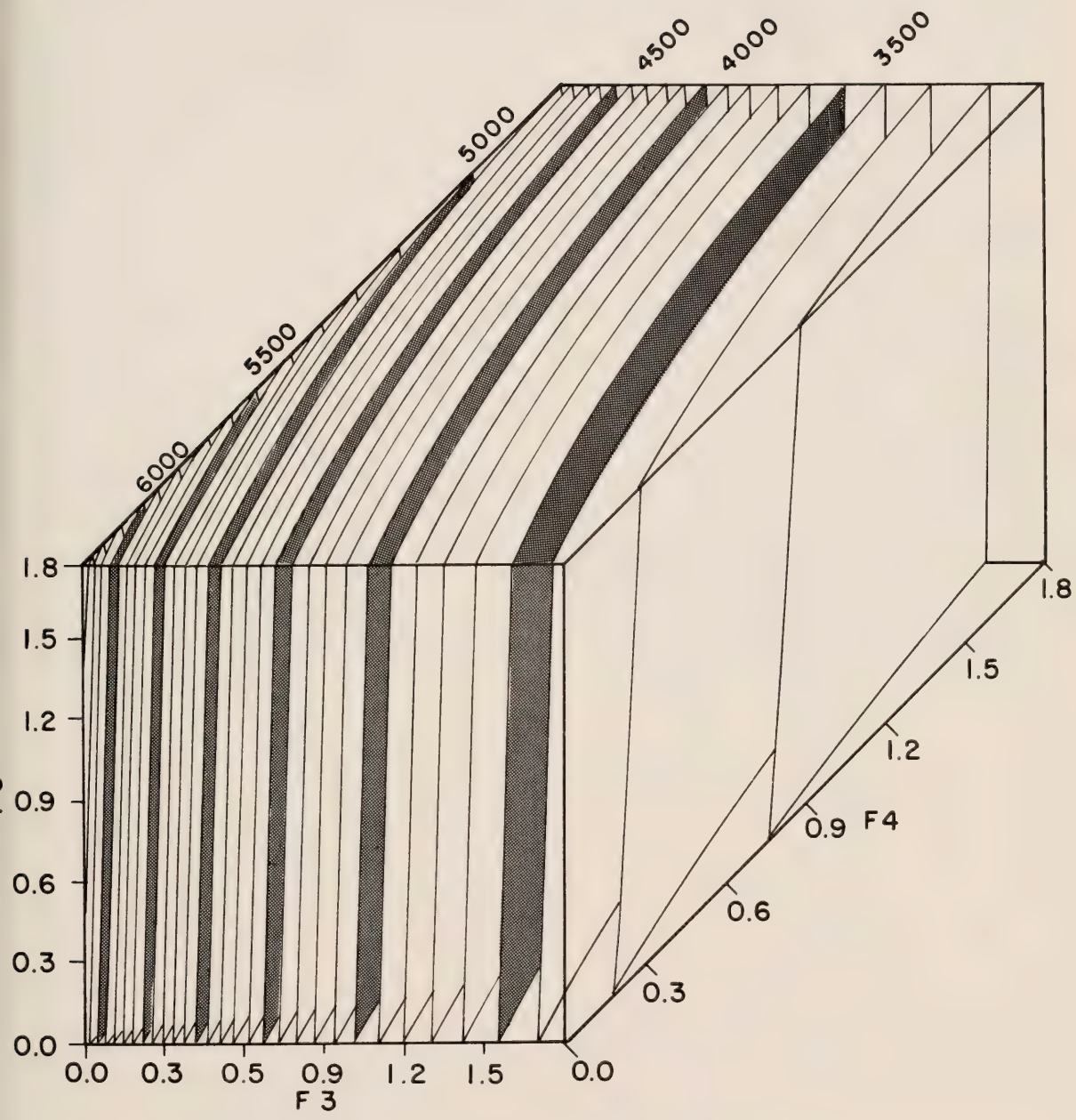

FIGURE 14.—Calculated total yield diagrams (in kilograms per 1,000 recruits) for the 1961 brood Kalama hatchery fall chinook salmon with constant natural mortality ($M = 0.24$), varying ocean troll fishing mortality rates (F_3, F_4, and F_5), and the proportion spawning and river fishing intensity remaining constant. Yields are shown by 100-kilogram plane intervals.

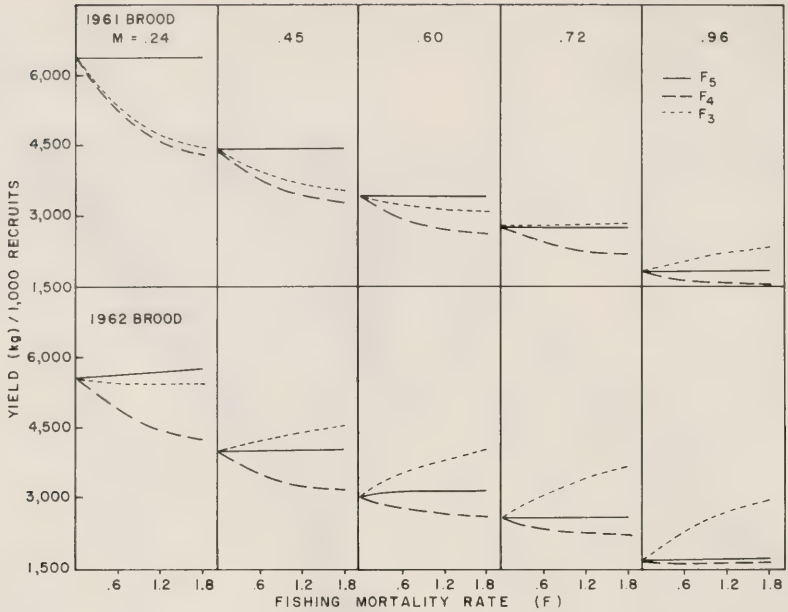

FIGURE 15.—Calculated total yields (in kilograms) for 1961 and 1962 brood Spring Creek hatchery fall chinook salmon for different natural mortality rates and fishing on only one age group at a time.

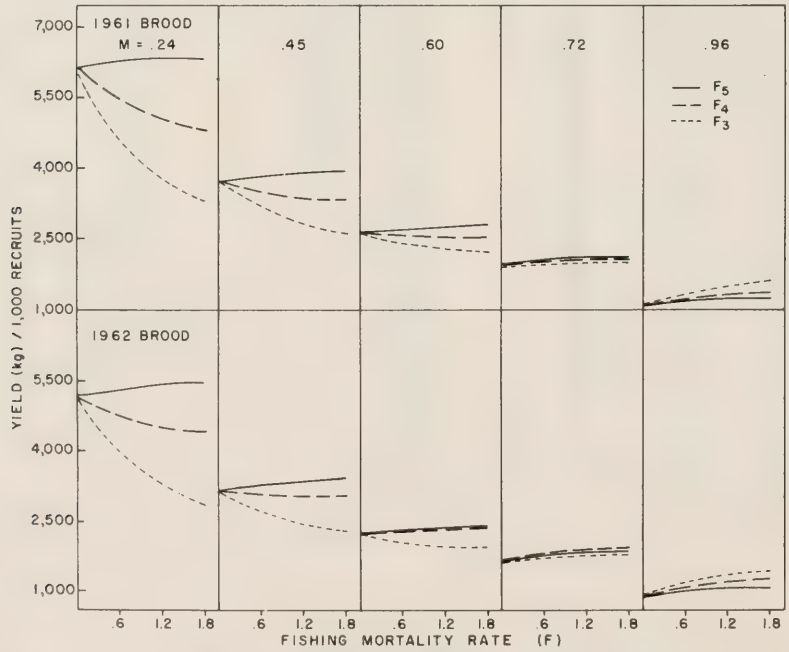

FIGURE 16.—Calculated total yields (in kilograms) for 1961 and 1962 brood Kalama hatchery fall chinook salmon for different natural mortality rates and fishing on only one age group at a time.

same as would be observed by reading along the F_3, F_4, and F_5 axes in Figures 13 and 14. It is apparent from these data that at any level of natural mortality (M_i), as fishing mortality is increased on the 5-year-old fish (F_5) (with F_3 and $F_4 = 0$), total yield increases, although slightly. For the Spring Creek data (Figure 15), any increase in F_4, with the other two F values $= 0$, would result in reduced yield. For Kalama fish (Figure 16), for both broods at $M = 0.72$ and higher, total yield would increase with an increase in any of the F values. In general, troll fishing on the age 3 and age 4 Spring Creek and Kalama fall chinook salmon tends to reduce total yield for M_i values less than 0.82, except for the 1962 brood Spring Creek fish. For these fish it appears that growth was insufficient to compensate for natural mortality losses of 4-year-old fish, even at a natural mortality rate of $M = 0.45$. Thus, yield was increased by harvesting them as 3-year-olds in the troll fishery (F_3).

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SELECTION OF SPAWNING SITES BY SOCKEYE SALMON IN SMALL STREAMS

DAVID T. HOOPES[1]

ABSTRACT

This study was undertaken in three small western Alaska streams to identify factors that influence selection of spawning sites by sockeye salmon. Temporal and spatial distribution patterns were relatively constant from year to year despite large fluctuations in the number of spawners. The selection of a spawning site was more closely related to composition of the stream bottom than to gradient, water depth and velocity, or cover.

The selection of spawning sites by salmon and the factors that influence selection bear directly on the problem of estimating the carrying capacities of spawning grounds. Such estimates cannot be developed for returning adults without knowledge of what constitutes an acceptable spawning area. In this study I relate the distribution of spawning sockeye salmon, *Oncorhynchus nerka*, in three small streams to the physical characteristics of the streams. The work reported was done at Brooks Lake, Alaska, in 1959, 1960, and 1961 and is one phase of an overall investigation by the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) on the freshwater ecology of sockeye salmon.

The three study streams, Hidden, Up-a-tree, and One Shot Creeks, are lateral[2] tributaries of Brooks Lake (Figure 1). Hidden Creek enters Brooks Lake in the southeastern shore about 10 km from the outlet, Brooks River. The other two streams lie between Brooks River and Hidden Creek. Up-a-tree Creek, the longest lateral stream in the Brooks Lake system, enters the lake at the southeastern corner; One Shot Creek, the shortest of the major spawning tributaries, flows into the lake on the south shore not far from Hidden Creek. Some physical features of the portions of the three streams accessible to salmon are presented in Table 1. Included in the table is the pool-riffle ratio, an indicator of the proportion of stream length composed of pools. What constitutes a pool is somewhat subjective, but I considered a pool to be a place where the stream was deeper and wider than average, the current was appreciably slower than immediately upstream or downstream, and hiding places for fish were more extensive than in adjacent parts of the stream.

The three streams were alike in two significant aspects—volume of flow and presence of beaver dams. Flows in each stream varied from 0.23 to 0.34 m^3s (cubic meter per second) (8.2 to 12.1 cfs) throughout the spawning season except for some short periods of higher flows during freshets. Beaver dams blocked the upstream migration of salmon except during brief periods of unusually high water.

DISTRIBUTION OF SPAWNERS

The distribution of adult sockeye salmon was observed closely and recorded from the time fish arrived off the stream mouths until they had all spawned. I recorded the number of fish ascending the streams each day and the distribution of spawners along each stream on an average of every 3 days.

Sockeye salmon school off the mouths of tributaries to Brooks Lake 1 to 3 weeks before ascending the streams to spawn (Hartman and

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[2] The term "lateral tributaries" refers to streams entering a lake from shores that lie roughly parallel to the lake's long axis.

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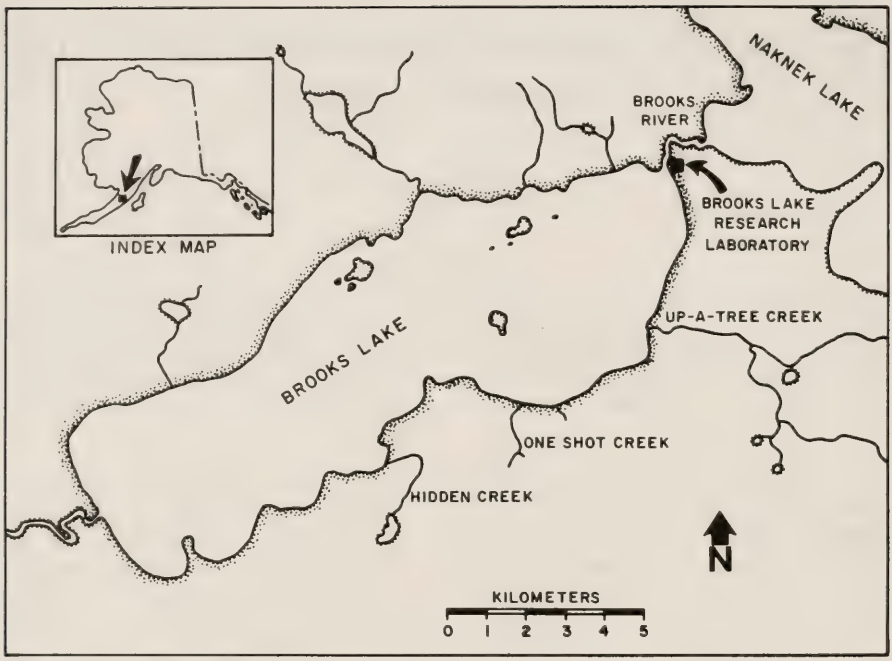

FIGURE 1.—Brooks Lake, Alaska, showing three lateral tributaries where spawning sockeye salmon were studied in 1959, 1960, and 1961.

Raleigh, 1964). I observed fish joining schools off the stream mouths even after some fish had entered the streams and begun spawning. These late-arriving fish usually spent several days in the school before they ascended the stream.

In some years all adult sockeye salmon that entered the study streams were passed through weirs. Weirs were operated at Up-a-tree and One Shot Creeks in 1961 (Table 2) and at Hidden Creek in 1959, 1960, and 1961 (Table 3). To insure that all fish in the run were counted, the weirs were closed when fish first appeared off the stream mouths. The fish were allowed to pass upstream through a counting gate whenever 10 or so appeared immediately downstream from the weir.

Although spawning sockeye salmon were constantly present in each study stream for several weeks, they tended to enter the streams in waves or pulses. Fish entered Hidden Creek in several distinct waves in 1959 and 1960 but not in 1961 (Table 3). However, the weir records for Up-a-tree and One Shot Creeks suggest the presence of more than one major influx of spawners in

TABLE 1.—Watershed area, total length, and physical characteristics of portions of streams accessible to salmon in Hidden, Up-a-tree, and One Shot Creeks, tributaries to Brooks Lake, Alaska.

Stream	Watershed area (km^2)	Total length (km)	Portion accessible to salmon					
			Stream length (km)	Range of stream width (m)	Pool-riffle ratio	Range of pool depths (cm)	Range of riffle depths (cm)	Percent gradient in spawning areas (*range*)
Hidden Creek	28	13	3.9	3-6.0	4:6	50- 80	15-30	0.74-1.45
Up-a-tree Creek	75	24	8.0	3-4.5	3:7	60-100	25-35	0.36-0.72
One Shot Creek	13	6.5	3.8	3-4.0	3:7	60- 90	25-35	0.84-1.30

TABLE 2.—Number of sockeye salmon passed upstream through the weirs each day and cumulative upstream count at Up-a-tree and One Shot Creeks, 1961.

Stream and date	No. of fish through weir	Cumulative count
Up-a-tree Creek		
July 28	1	1
29	0	1
30	135	136
		[1]521
31	[2]121	642
Aug. 1	1	643
2	35	678
3	0	678
4	0	678
5	10	688
6	3	691
7	0	691
8	26	717
9	59	776
10	0	776
11	9	785
12	2	787
13	3	790
14	19	809
15	10	819
16	0	819
17	12	831
18	0	831
19	0	831
20	0	831
21	0	831
22	0	831
23	0	831
24	0	831
25	0	831
26	0	831
27	1	832

Stream and date	No. of fish through weir	Cumulative count
One Shot Creek		
July 30	1	1
31	10	11
Aug. 1	14	25
2	146	171
3	6	177
4	9	186
5	3	189
6	0	189
7	0	189
8	85	274
9	1	275
10	0	275
11	4	279
12	11	290
13	0	290
14	0	290
15	1	291
16	0	291
17	0	291
18	5	296
19	0	296
20	4	300
21	0	300
22	0	300
23	0	300
24	0	300
25	0	300
26	0	300
27	1	301
28	2	303
29	0	303
30	2	305

[1] At 7:30 a.m. on July 30 the Up-a-tree Creek weir was washed out because of high water. The weir was replaced and a stream survey made on July 31 after the water receded and cleared. An estimate of 521 fish was obtained. This figure was used for subsequent cumulative counts.
[2] Counted upstream after survey.

these two streams in 1961 (Table 2). Three distinct waves of spawners were observed in studies on nearby Brooks River by Hartman, Merrell, and Painter (1964).

The distribution of spawners over the length of each stream was determined from repeated counts of occupied redds in survey sections which were established for measuring stream gradients.[3] The counts were summed by section and totaled for the entire stream. The percentage of this total occurring in each section was calculated for the year, and these percentages were used as indicators of the distribution of each year's run. Distribution was not uniform among the three study streams during the 3 years of this study but was generally consistent for each stream (Figures 2, 3, 4) despite marked differences between years in the number of spawners (Table 4).

In 1959, when occupied redd sites were counted at 2-day intervals, the distribution of spawners in Hidden Creek changed very little after the first week. Counts were combined to show the similarity in distribution of occupied redds at the end of the first, second, and third week of spawning (Figure 5). By the end of the first week (early period), 2,625 sockeye salmon had ascended the stream to select redd sites and spawn. An additional 1,239 fish entered and began to spawn during the second week (middle period), and 694 more entered during the third week (late period). Thus, substantial numbers

[3] These survey sections will be described in more detail later. They consist of 100- to 200-m-long segments of stream channel extending from the mouths of the study streams to the first beaver dam judged to be normally impassable to migrating salmon.

TABLE 3.—Number of sockeye salmon passed upstream through the weir each day and cumulative upstream count at Hidden Creek, 1959, 1960, and 1961.

Date	1959		1960		1961	
	No. of fish through weir	Cumulative count	No. of fish through weir	Cumulative count	No. of fish through weir	Cumulative count
August						
9	--	--	--	--	38	38
10	1,240	1,240	--	--	0	38
11	0	1,240	--	--	39	77
12	0	1,240	--	--	1	78
13	547	1,787	--	--	383	461
14	40	1,827	23	23	417	878
15	574	2,401	1,216	1,239	0	878
16	224	2,625	269	1,508	0	878
17	0	2,625	6	1,514	8	886
18	1,217	3,842	42	1,556	130	1,016
19	0	3,842	0	1,556	0	1,016
20	0	3,842	0	1,556	0	1,016
21	0	3,842	319	1,875	0	1,016
22	22	3,864	158	2,033	0	1,016
23	0	3,864	0	2,033	0	1,016
24	0	3,864	110	2,143	0	1,016
25	0	3,864	43	2,186	7	1,023
26	0	3,864	1	2,187	46	1,069
27	0	3,864	15	2,202	3	1,072
28	694	4,558	37	2,239	0	1,072
29	--	--	10	2,249	1	1,073
30	--	--	26	2,275	0	1,073
31	--	--	--	--	1	1,074
September						
1	--	--	--	--	4	1,078
2	--	--	--	--	0	1,078
3	--	--	--	--	0	1,078
4	--	--	--	--	0	1,078
5	--	--	--	--	13	1,091

TABLE 4.—Sockeye salmon escapements into Hidden, Up-a-tree, and One Shot Creeks in 1959, 1960, and 1961.

Stream and year	Method of enumeration	No. of fish in escapement[1]
Hidden Creek		
1959	Weir count	4,558
1960	Weir count	2,275
1961	Weir count	1,078
Up-a-tree Creek		
1959	Stream survey[2]	542
1960	Stream survey	1,334
1961	Stream survey and weir	653 (832)
One Shot Creek		
1959	Stream survey	246
1960	Stream survey	269
1961	Stream survey and weir	221 (305)

[1] Figures in parentheses are weir counts.
[2] Highest single count during any one season.

of fish ascended the stream and occupied redd sites while other fish were already spawning. Some late fish spawned adjacent to previous arrivals, and others continued on to the upstream spawning areas. This distribution of spawners was not measurably altered by differences in their numbers, as evidenced by the distribution throughout the season of the considerably fewer fish in 1961.

Although the distribution of spawners from year to year varied more in Up-a-tree than in Hidden Creek, Up-a-tree Creek had areas of consistently high and consistently low spawning density (Figure 3). More spawners entered Up-a-tree Creek in 1960 than in 1959 or 1961, and the 1960 spawners were distributed more uniformly along a greater length of stream than either the 1959 or 1961 spawners. In 1961, relatively few fish spawned in the lower sections of the stream.

The distribution and number of spawners in One Shot Creek was similar for the 3 years of the study (Figure 4, Table 4)—here spawners consistently concentrated in the upper and lower ends of the stream.

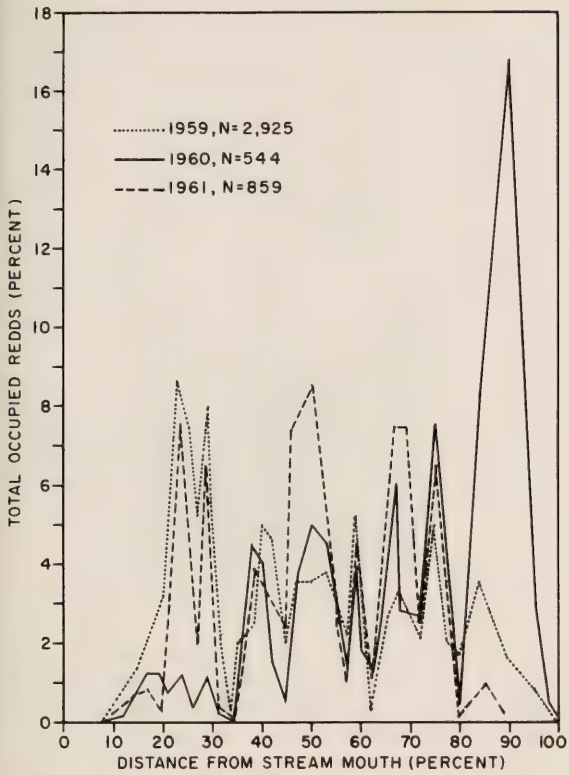

FIGURE 2.—Distribution of redds occupied by sockeye salmon in Hidden Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

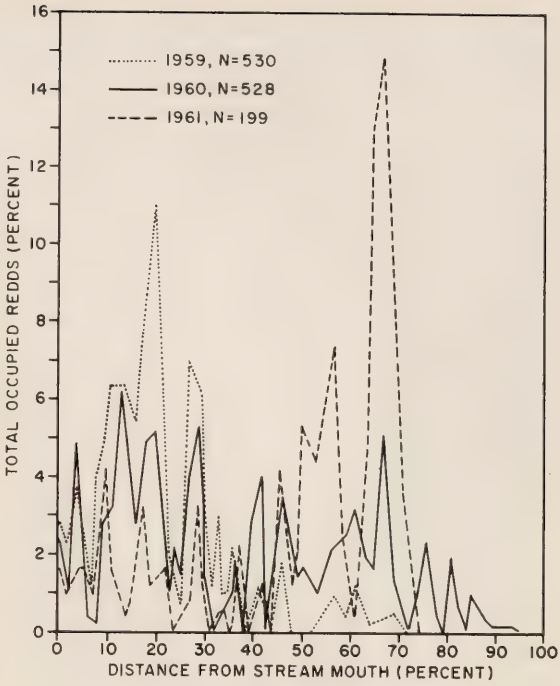

FIGURE 3.—Distribution of redds occupied by sockeye salmon in Up-a-tree Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

PHYSICAL CHARACTERISTICS OF STUDY STREAMS IN RELATION TO SPAWNING

To determine relationships between the location of spawning sites and physical characteristics of the streams, I measured the gradient, size composition of the bottom materials, and water depth and velocity of spawning areas in the three streams. Velocity and volume of streamflow, stream width, and stream gradient are known to affect the size composition of materials in the streambed, but velocity is considered to be the dominant factor (Krumbein and Pettijohn, 1938; Rubey, 1938; Hjulstrom, 1939; Krumbein and Sloss, 1951). A reduction in stream gradient is accompanied by a reduction in water velocity and in the average size of bottom particles.

STREAM GRADIENT

Gradients were measured in each study stream from the mouth to the first beaver dam judged normally impassable to migrating salmon. Gradients were calculated between convenient points (stations) that were 100 to 200 m apart along the stream. The relative elevation of the water surface was measured with a surveyor's level, and the distance between stations was measured along the center of the streambed with a surveyor's chain. Stream width was also measured at each station. The survey sections were numbered consecutively upstream from the mouth of each creek.

Survey sections were often too long to reveal variations in gradient and distribution of spawn-

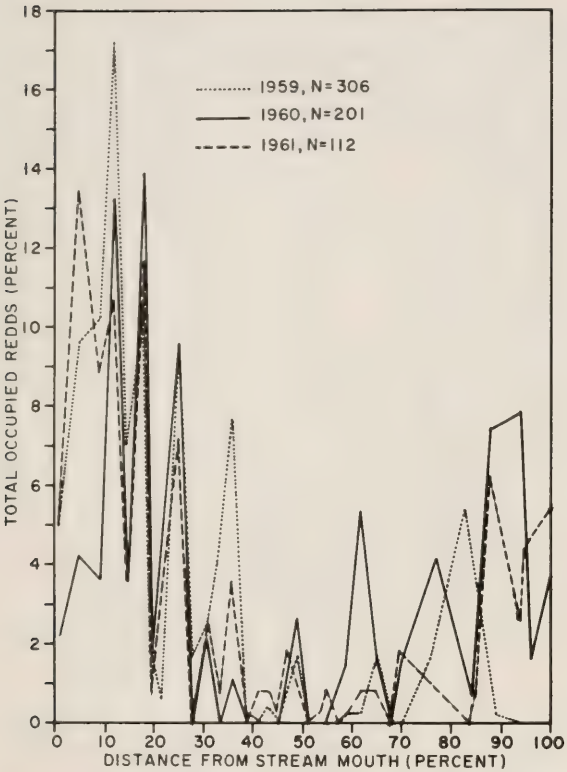

FIGURE 4.—Distribution of redds occupied by sockeye salmon in One Shot Creek, Brooks Lake, Alaska, during the 1959, 1960, and 1961 spawning seasons.

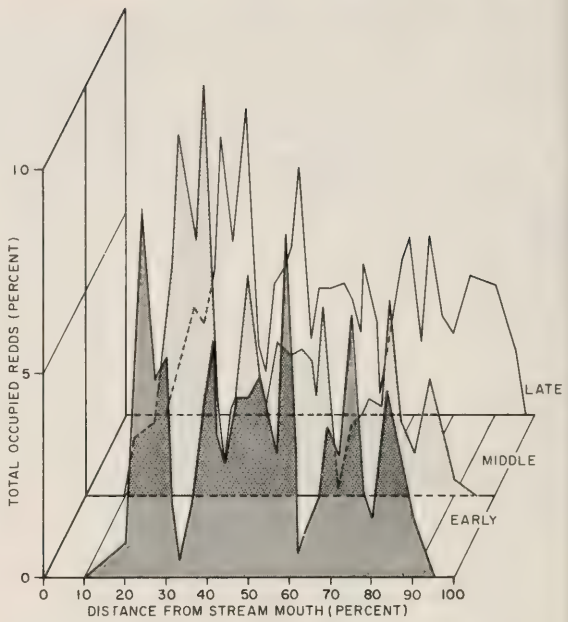

FIGURE 5.—Temporal and spatial distribution of redds occupied by sockeye salmon during the early, middle, and late periods of the 1959 spawning season in Hidden Creek, Brooks Lake, Alaska.

ers in great detail. For example, some had so many steep runs and falls that the average gradient appeared to be too high for spawning, although the sections contained one or two short reaches of stream with gradients acceptable to spawning fish. Other sections had long reaches of generally too low gradient but had one or two short steep falls, so that little acceptable spawning ground was actually available even though the average gradient appeared suitable for spawning. Despite these problems in methodology, after comparing the density of spawning females and stream gradients section by section in the three study streams for all 3 years, I found that little or no spawning occurred in areas having average gradients of less than 0.5% or more than 2.0%.

SIZE OF STREAMBED MATERIALS IN SELECTED SECTIONS

I made detailed studies of bottom composition in eight of the sections surveyed for gradient.[4] Sections were selected for these detailed studies on the basis of their relative amounts of use by spawning salmon so that areas having high and low spawning densities could be compared. Two sections with high and two with low densities of spawners were selected in Hidden Creek, and one each was selected in Up-a-tree and One Shot Creeks.

From six to nine samples of the streambed were collected in each of the eight sections. The samples were taken from both pools and riffles at locations where salmon spawned in 1959. Each sample consisted of the top 20 to 30 cm of bottom materials (gravel and sand) from an area 1 m^2. The material was removed from the

[4] Observations were also made on water depth and velocity and availability of streambank cover.

streambed with a shovel and placed in a cotton soil sample bag. It was later washed into individual 19-liter tins, drained, and allowed to air dry. The dried samples were separated into 10 size classes by passing them through a stacked series of square-meshed 20-cm U.S. Standard sieves. After the sample was placed on the top sieve, the series was agitated for 10 min in a hand-powered portable sieve shaker. The materials retained on each sieve were weighed to the nearest gram on a triple-beam trip scale.

I describe the particle size distribution of the streambed by relating the percent of the total sample weight retained on each sieve to the logarithm of its mesh size. This method of analysis is described more fully by Spangler (1951) and by the American Society for Testing Materials (1958).

Because the particle composition of streambed samples from pools and riffles was so similar within each section, I combined the data by section. I then derived a cumulative size distribution for each section by summing the weights retained by each sieve size in all samples for a section. These data were used to construct cumulative distribution curves with which I could compare the composition of the stream bottom in sections of high spawning density (Figure 6) with that in sections of low spawning density (Figure 7).

The curves for sections of high spawning density (Figure 6) show that bottom composition was quite similar in all three streams. The only difference among the four sections was the slightly higher percentage of small particles and the somewhat lower percentage of large particles in section 9 of Hidden Creek, as evidenced by the lateral displacement toward the left of the composition curve for this section.

The cumulative curves for sections with low spawning density (Figure 7) showed that particle size distribution was similar in three of the sections (one from each stream) but quite different in the fourth section (Hidden Creek, 2). It is clear that spawner density was low in Hidden Creek in areas where particle sizes were either very large or very small.

Sockeye salmon spawned most frequently in areas where the particles were intermediate in size. In sections of high spawning density and intermediate gradient, cobbles larger than 7.6 cm in diameter made up about 6% of the bottom, cobbles from 2.5 to 7.6 cm about 50%, particles 1.3 to 2.5 cm about 20%, and particles less than 1.3 cm the remainder (Figure 8A). The bottom in sections of low spawning density and high gradient was made up of almost 40% cobbles exceeding 7.6 cm in diameter and contained very little material less than 2.5 cm in diameter (Figure 8B). The bottom in sections of low spawn-

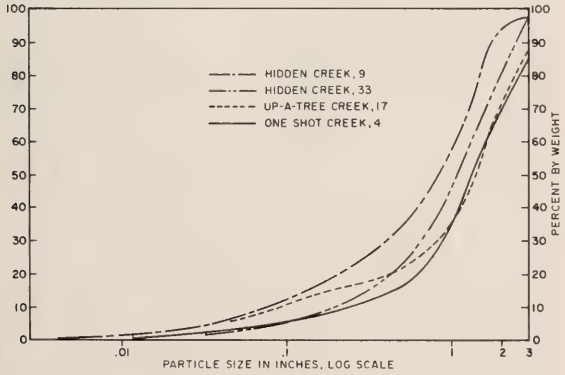

FIGURE 6.—Curves of cumulative particle size distribution in four sections with high-spawning density, Hidden Creek sections 9 and 33, Up-a-tree Creek section 17, and One Shot Creek section 4. All four sections had intermediate stream gradients.

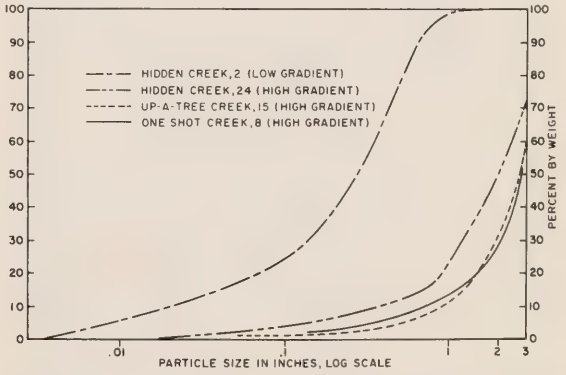

FIGURE 7.—Curves of cumulative particle size distribution in four sections with low-spawning density, Hidden Creek sections 2 and 24, Up-a-tree Creek section 15, and One Shot Creek section 8. All of the sections had high gradients except Hidden Creek section 2, which had low.

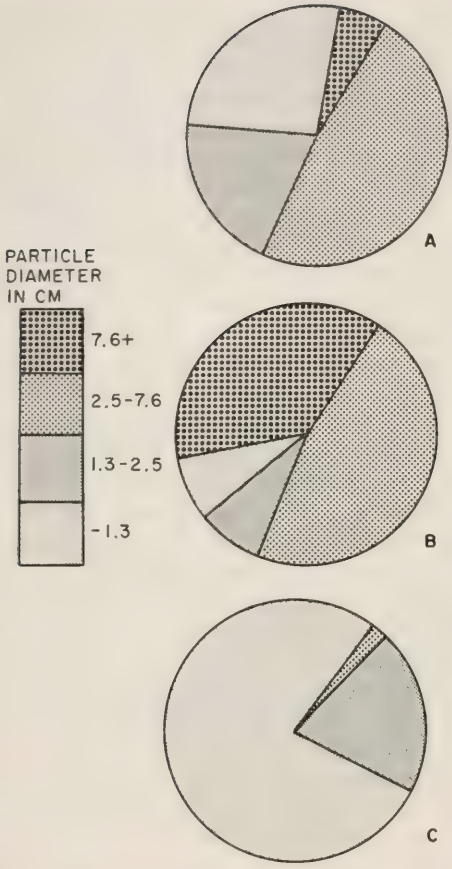

FIGURE 8.—Particle composition by percent weight of bottom materials in study sections having (A) high spawning density and intermediate gradient, (B) low spawning density and high gradient, and (C) low spawning density and low gradient.

ing density and low gradient contained 80% particles under 1.3 cm in diameter (Figure 8C).

WATER DEPTH AND VELOCITY

Water depth and velocity were measured in 1960 in each of the eight study sections (Table 5). Three to five transects about equidistant from each other were laid out across the stream in each section. Velocity and depth were measured at about 0.3-m intervals along these transects with a Gurley impeller-type current meter[5] mounted on a graduated rod and set at 12 cm above the streambed, described as "fish depth" for Pacific salmon.[6] Volume of flow was computed from the velocity and depth data collected. The values presented are assumed to reflect conditions normally encountered by fish selecting spawning sites in the study sections, although pronounced changes in water depth and velocity may occur briefly during the spawning season as a result of heavy rains. Sections with high and low densities of spawners often had similar water depths and velocities (Table 5: Depths—Hidden Creek, section 9 versus 24; One Shot Creek, section 4 versus 8. Velocities—Hidden Creek sections 9 and 33 versus Up-a-tree Creek section 15 and One Shot Creek section 8).

[5] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

[6] J. S. Chambers, R. T. Pressey, J. R. Donaldson, and W. R. McKinley. Washington State Department of Fisheries, Annual Report, 1954, submitted to U.S. Army Corps of Engineers, 145 p.

TABLE 5.—Average depth, velocity, and volume of flow in sections of high and low spawning densities of Hidden, Up-a-tree, and One Shot Creeks, Brooks Lake, Alaska, 1960.

Stream and section	Level of spawning density	Average depth (cm)	Water velocity (mps)	(fps)	Volume of flow (m^3s)	(cfs)
Hidden Creek						
9	High	15	0.59	1.9	0.27	9.6
33	High	23	0.45	1.5	0.31	11.1
24	Low	15	0.70	2.3	0.25	8.9
2	Low	28	0.39	1.3	0.28	10.0
Up-a-tree Creek						
17	High	24	0.36	1.2	0.29	10.3
15	Low	23	0.47	1.5	0.31	11.1
One Shot Creek						
4	High	32	0.35	1.1	0.37	13.2
8	Low	28	0.54	1.8	0.44	15.7

FACTORS AFFECTING SPAWNING SITE SELECTION

Salmon and trout usually spawn in a specific type of microenvironment within a broadly uniform environment. One such type of microenvironment occurs at the downstream ends or tails of pools, just upstream from the point where the flow breaks over the lip of the pool into the riffle below (Needham and Taft, 1934; Schultz and students, 1935; Smith, 1941; White, 1942; Briggs, 1953; Shapovalov and Taft, 1954). Riffles may also contain microenvironments attractive to spawning salmon[7] (Belding, 1934; Burner, 1951; Needham and Vaughan, 1952; Briggs, 1953; see also footnote 6.)

Variations in streambed slope are important in the selection of spawning sites because these variations cause exchange in intragravel and stream water (Vaux, 1962) and affect the stability of the bottom. In pools, spawning sites were usually located where the bottom sloped upward slightly in the direction of flow, as in pool tails. Even in riffles, fish observed during this study seldom constructed redds where the bottom sloped steeply but rather chose gently sloping sites where the excavated tailspill provided a slight rise. The preferred streambed was also nearly level across the stream, although moderate to steep lateral inclines were occasionally used in crowded areas.

In 1959, sockeye salmon first entered and began spawning in Hidden Creek on August 11. On August 13, I marked 14 redds in an area of high spawning density after taking detailed notes on the exact location of each spawning site and the features of the immediate environment. I assumed that the first fish in an area selected the preferred sites, so that these 14 sites represented preferred habitat. All of the sites were at or near the tails of pools and along the bank adjacent to the main streamflow. I observed the sites until August 25, when high water precluded further study.

Observations in the immediate vicinity of the 14 study redds showed that late-arriving fish spawned upstream from the initial redd at the tail of each pool. When the pool was filled with redds for its entire length and pool width permitted two or more redds side by side, late arrivals chose spawning sites sequentially upstream, again beginning at the tail but across the stream from the original site. No salmon spawned in unstable gravels usually associated with the shallow sides of pools.

Riffles made up 60 to 70% of the stream length accessible to salmon in the three study streams, and many fish spawned in these riffles. As in the pools, spawning salmon preferred definite parts of the riffles. The first fish invariably chose sites along the deeper side and higher bank. Salmon also preferred certain riffles over others. Short riffles with water of moderate depth and flow were used as readily as pool tails. Long shallow riffles with some cover along adjacent banks were occupied next. The last sites used were those in long shallow riffles without nearby pools or cover.

The significance of cover in the selection of a spawning site by sockeye salmon is hard to evaluate. Hourston and MacKinnon (1957) found that pink salmon, *O. gorbuscha*, spawning in an artificial channel selected sites adjacent to cover rather than those distant from cover. I frequently observed that sockeye salmon, especially those that arrived early when a wide choice of sites was available, selected a site that had good cover. The absence of cover did not necessarily prevent early spawners from selecting a particular site, but given two adjacent locations apparently equal with regard to water depth and flow and gravel composition, the fish tended to select the site nearer to cover. Favored sites were near deeply undercut banks, banks overhung with tall grass and herbaceous plants, holes washed under tree roots, log and brush jams, and deep pools.

Cover that attracts alarmed fish may not actually afford protection, because concealment alone does not insure safety. I have observed brown bears, *Ursus gyas*, systematically search for salmon under overhanging vegetation and undercut banks. In my three study streams,

[7] J. S. Chambers, G. H. Allen, and R. T. Pressey. Washington State Department of Fisheries, Annual Report, 1955, submitted to U.S. Army Corps of Engineers, 175 p.

cover that would protect a salmon from bears was quite scant, and even when such cover was available, alarmed fish often sought the shaded area provided by overhanging herbs and grasses as refuge rather than places of comparatively greater security such as undercut banks and logs.

The selection of a site by a spawning sockeye salmon seemed to be more closely related to the composition of the stream bottom than to any other single factor studied. Work done with fish closely related to salmon supports this view (Hobbs, 1940; Fabricius, 1950; Fabricius and Gustafson, 1954; Needham, 1961). This preference by salmon for areas having bottom materials of intermediate composition explains why the density of spawners was high in sections with moderate gradient and low in sections with either high or low gradient. When more desirable bottom material was lacking, fish spawned in excessively coarse material (higher gradients) before excessively fine (lower gradients). In this respect, my observations indicated that gradient was related to the selection of spawning sites by sockeye salmon. The observations by Trautman (1942) and Huet (1949, 1959) showing that distribution of several species of fish permanently resident in lotic environments is closely related to stream gradient may well have resulted from a preference by those fish for a particular substrate.

Factors other than physical conditions in the spawning grounds may also influence the selection of redd sites by sockeye salmon. Briggs (1955) stated that among anadromous fishes, the earliest arrivals in a particular spawning tributary traveled to the most distant spawning grounds and the later arrivals occupied areas closer to the stream mouth. In the three streams I studied, however, early arrivals did not necessarily ascend to the uppermost spawning areas. Moreover, the sites selected by later arrivals often were located between sites chosen by the earlier spawners.

The female sockeye salmon selects the spawning site, usually near other spawners (Noble, 1938). The presence and stimulation of other spawners may be necessary for successful spawning even though much effort is expended in territorial defense. I seldom saw single spawning pairs but observed rather that fish tended to form more or less isolated groups of several pairs. How much of this behavior is due to preference for certain physical characteristics of the spawning grounds and how much to innate social behavior is not known.

SUMMARY

1. Spawning site selection by sockeye salmon in three small lateral tributaries entering Brooks Lake, Alaska, was studied from 1959 through 1961.

2. Several waves of sockeye salmon spawners ascended the principal study stream in 1959 and 1960 when the numbers of fish were moderate and high but not in 1961, a year of relatively few fish.

3. Both temporal and spatial distribution patterns were defined and found to be relatively constant despite large fluctuations in the number of spawners.

4. The distribution of spawning fish was correlated with stream gradients. Little or no spawning occurred in areas having gradients of less than 0.5% or more than 2.0%.

5. In preferred spawning areas, cobbles from 2.5 to 7.6 cm in diameter made up about 50% of the bottom, materials 1.3 to 2.5 cm about 25%, and particles less than 1.3 cm the remainder.

6. Spawner distribution was more closely related to the composition of the stream bottom than to any other single factor studied.

7. Given two adjacent locations equally desirable with regard to hydrological conditions and bottom composition, sockeye salmon tended to select the site with the most nearby cover and concealment.

8. Early arrivals did not necessarily use the uppermost spawning areas, and later arrivals primarily filled in acceptable areas already in use.

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REDESCRIPTION OF SOME SPECIES OF *CHONE* KRÖYER AND *EUCHONE* MALMGREN, AND THREE NEW SPECIES (SABELLIDAE, POLYCHAETA)[1]

KARL BANSE[2]

ABSTRACT

Generic diagnoses are given for *Chone* (syn. *Megachone*) and *Euchone*. Redescriptions and additions to the descriptions, in part based on study of the types, are provided for some species, *Chone aurantiaca* (new combination), *C. duneri* (syn. *C. bimaculata*), *C. ecaudata* (syn. *C. minuta*), *C. eniwetokensis* (new combination), *C. gracilis*, *C. infundibuliformis* (syn. *C. teres*), *C. magna*, *C. mollis*, *C. paucibranchiata*, *Euchone alicaudata*, *E. analis*, *E. capensis*, *E. elegans*, *E. papillosa*, and *E. rubrocincta*. Three new species, *Chone albocincta*, *Chone veleronis*, and *Euchone velifera* are described. The number of lobes of the collar is rejected for the Sabellidae as a character on the generic level; the diagnostic value of the palmate membrane is discussed.

The sabellid polychaetes are filter feeders which usually live in permanent tubes. Two genera, *Chone* Kröyer and *Euchone* Malmgren, which occur worldwide, are treated here taxonomically. The length of species of *Chone* ranges from 2.5 mm to almost 10 cm, that of species of *Euchone* from a few millimeters to a few centimeters. Some species are quite common on sandy or muddy bottoms (cf. McIntosh, 1916; Hartman, 1944b; Kühlmorgen-Hille, 1963); at least some species are eaten by fishes (McIntosh, 1916; Berkeley and Berkeley, 1954).

The study was initiated because of difficulties in identifying large species of *Chone* in the Synoptic Collection of the Friday Harbor Laboratories, University of Washington. This led to reexaminations of some types and other specimens primarily from the North Pacific and North Atlantic Oceans. The results are an emendation of the generic diagnosis of *Chone*, including the placement of *Megachone* Johnson in *Chone*, the redescription or improvement of the knowledge of some previously known species, and the erection of three new species. Because material of several large species of *Euchone* was at hand, additions to their descriptions are also included, the generic diagnosis is emended, and a new species is described.

Of general taxonomic interest is the discovery of a new species of *Euchone*, *E. velifera*, which has a ventrally deeply incised collar with an additional pair of lateral notches (Figure 12a). A collar that is ventrally moderately incised is known also for *E. papillosa* (Sars) and *E. capensis* Day (Figure 11n). The species otherwise agree fully with the characters of *Euchone*. Similarly, *Chone trilobata* Gallardo has deep lateral notches in its collar but otherwise is typical. Especially the occurrence of bilobed collars in species of *Euchone*, a genus uniquely characterized by the anal depression, provides further evidence in support of Johansson's (1927) strong criticism of the attempt by Bush (1904) to make the collar a character of major importance in distinguishing genera among the Sabellidae. Consequently, genera like *Pseudopotamilla* Bush, separated from *Potamilla* Malmgren only by differences in the collar, should not be maintained. In view of the fact that not all *Euchone* species have a palmate membrane, the question is dis-

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cussed (p. 461) whether the character should be used in the generic diagnosis for the closely related *Chone*.

The observations on some primitive characters in Sabellidae by Banse (1970), especially in regard to the abdominal uncini, are supported by the observations on the species discussed below. To those characters may be added the glandular girdle on the second setiger which is common to all species of *Chone* and *Euchone* and is found also in the sabellid genera *Jasmineira* Langerhans and *Myxicola* Koch. It is considered to be a phylogenetically primitive character not only because of the position of *Chone* and *Euchone* within the family but also because similar girdles occur in other families (e.g., Southern, 1914, for Terebellidae).

METHODS

Because the form of the uncini can vary considerably within the abdomen, the shape of the setae in the anterior abdominal setigers is stressed in the following descriptions. The accessory teeth above the main fang of an uncinus are arranged in several vertical "columns" appearing in side view as horizontal (not strictly so) "rows." The nomenclature for the abdominal segments in *Euchone* follows Banse (1970). The procedure for staining with methyl green introduced by Hofsommer (1913) is described in the same article.

The following abbreviations are used: AHF for Allan Hancock Foundation, University of Southern California, Los Angeles, Calif.; FHL for Friday Harbor Laboratories, University of Washington, Friday Harbor, Wash.; MCZ for Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; NMI for National Museum of Ireland, Dublin; PMNH for Peabody Museum of Natural History, New Haven, Conn.; SMNH for Swedish State Museum of Natural History, Stockholm; SEP for Systematics-Ecology Program, Marine Biological Laboratory, Woods Hole, Mass.; UCT for University of Cape Town; USNM for U.S. National Museum of Natural History, Washington, D.C.; ZMC for Zoological Museum of the University of Copenhagen; and ZMO for Zoological Museum, University of Oslo. When not noted otherwise, the specimens are in my collection.

SPECIAL PART

CHONE KRÖYER, 1856 EMENDED

CHONE Kröyer, 1856, p. 13.- Sars, 1862, p. 119.- Malmgren, 1866, p. 404.- Langerhans, 1881, p. 111.- Saint-Joseph, 1894, p. 250.- Bush, 1904, p. 189.- Hofsommer, 1913, p. 332.- McIntosh, 1923, p. 287.- Fauvel, 1927, p. 334.- Berkeley and Berkeley, 1952, p. 122.- Ushakov, 1955, p. 417.- Day, 1967, p. 776.
PARACHONIA Kinberg, 1867, p. 355.
MEGACHONE Johnson, 1901, p. 430.
METACHONE Bush, 1904, p. 190, 216.

Type species: *Chone infundibuliformis* Kröyer (cf. Bush, 1904).

Diagnosis: Sabellidae with semicircular branchial lobes united by palmate membrane. Collar conspicuous. Postsetal girdle of glands on second setiger. Ventral shields sometimes present. Ends of abdomen of typical sabellid form. Three types of thoracic notosetae: upper, anterior ones limbate, sometimes in two series of different length; lower, anterior ones narrowly limbate (bayonet-type); and lower, posterior ones spatulate or subspatulate. Thoracic neuropodial uncini long-handled, acicular. Abdominal notopodial uncini avicular, with square or rounded bases; abdominal neurosetae limbate.

Remarks: The emended diagnosis comprises the same species as previously (cf. Hartman, 1959, 1965, and below), although it contains as new characters the postsetal girdle of glands, the ventral shields, the bayonet-like setae, and the qualification "or subspatulate setae." The usual occurrence of ventral nude filaments in the branchial crown, the occasional presence of otocysts, and the diagnostic characters pertaining to the family are omitted. There are usually eight thoracic setigers; very rarely a specimen deviates from this number.

Parachonia has been included in *Chone* by Johannson (1927), *Metachone* by Fauvel (1927; see also Hartman, 1942b).

The type species of *Megachone* Johnson, *M. aurantiaca*, is redescribed below, based in part on the holotype. Contrary to the statement by Johnson (1901), the species does have ordinary spatulate setae in the thoracic notopodia and thus agrees in every respect with *Chone*.

The diagnosis as given has one weakness: The original reason of Kröyer (1856) in creating *Chone* was the funnel-like appearance of the lophophores, or branchial crown, caused by the palmate membrane. This membrane is not of so unique value as a generic character as originally thought. Sars (1862) was the first to point out that the membrane occurs also in other genera. More important is that it may be present or absent in the closely related *Euchone* (Banse, 1970). If the palmate membrane were considered also in *Chone* as a specific character, *Dialychone* Claparède would become a synonym of *Chone* (cf. Fauvel, 1927). For the practical need of identification, however, considerable difficulties would result. For example, a large species of *Oriopsis* Caullery and Mesnil (cf. *O. rivularis* Annenkova, with bayonet-type thoracic notosetae) would externally be distinguishable from *Chone* only by the absence of the postsetal glandular girdle on the second setiger. Anatomically, *Oriopsis* would, of course, be quite different because it belongs to the thoracogoneate Fabriciinae (Zenkevitch, 1925) with their unique gonoducts. Because eggs may occur in thoracic segments also in abdominogoneate sabellids (cf. *Euchone hancocki* Banse), identification without anatomical study may sometimes not be possible. In view of these problems it seems wise to define *Chone* as above until intensive anatomical studies of representatives of the various subgroups of Fabriciinae have been made. These may yield a more natural and hence more convincing system than is available now.

Among most species of *Chone*, the collar has a very narrow dorsal gap. *C. trilobata* has a collar with deep lateral notches. The bayonet-type setae (also called basal or geniculate setae) were described in some species by previous authors (cf. Fauvel, 1927; Eliason, 1962) but seem to be present in all members of the genus. The lower posterior thoracic notosetae are sometimes subspatulate, as in *C. filicaudata* Southern and *C. eniwetokensis* (Reish).

The abdominal uncini with square bases and few teeth, thought to be typical for *Chone* (cf. Figure 1k) are found in many species only in anterior abdominal segments, as is the case also in *Euchone* (Banse, 1970). The uncini of posterior setigers can have instead small rounded bases and a high crown of accessory teeth (cf. Figure 6i). Such uncini occur similarly in other genera of Sabellidae and in related families and are thus phylogenetically more primitive than the typical hooks of *Chone*. Further, they can be present in the same tori together with typical ones, as in *C. ecaudata* Moore and *C. albocincta* new species (cf. *Euchone elegans*). Their position shows that ontogenetically they have been formed first. Also this points to the primitiveness of the posterior uncini. Likewise Okuda (1946) has shown in a developmental study of *?C. ecaudata* (see below) that the abdominal uncini first formed are of the primitive type and similar to those found, for example, in *Oriopsis;* initially they occur even in the thorax.

In spite of the clarification of diagnostic characters, very little can yet be said about the relations among species of *Chone*. Certainly, species with ventral shields are more primitive than those with fully glandularized epidermes because reasonably primitive Sabellidae should have shields. Significantly, the typical abdominal uncini with square bases seem to be present throughout the abdomen only among *Chone* species having a fully glandularized epidermis (possibly also in *C. eniwetokensis*, according to Reish, 1968).

CHONE INFUNDIBULIFORMIS KRÖYER

Figure 1

CHONE INFUNDIBULIFORMIS Kröyer, 1856, p. 33.- Malmgren, 1866, p. 404; 1867, p. 214.- Hofsommer, 1913, p. 332.- McIntosh, 1916, p. 35, 39.- Imajima, 1961, p. 98.- Hartmann-Schröder, 1971, p. 520. See also p. 465.

CHONE TERES Bush, 1904, p. 215.- Hartman, 1942b, p. 87; 1959, p. 539.

not *CHONE TERES*.- Okuda, 1934, p. 236; 1946, p. 171.- Imajima and Hartman, 1964, p. 365 (for these three references see *C. ecaudata*).- Chlebovich, 1961, p. 231 (see Remarks).

Diagnosis: A large *Chone* species without ventral shields. Branchial basis as long as level collar. About 20 pairs of radioles, connected for two-thirds to three-fourths of length by palmate membrane, with free ends very short and broad. First bundle of setae of normal size, inserted more dorsally than following notosetae.

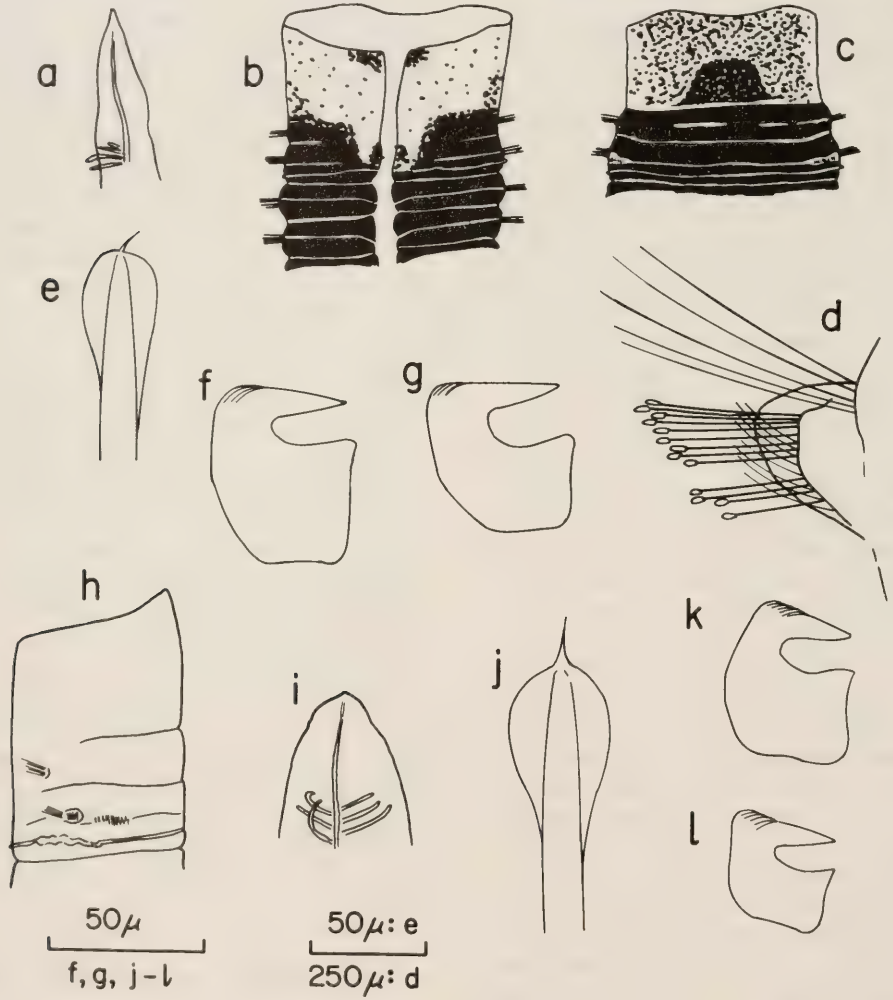

FIGURE 1.—*Chone infundibuliformis*; a from Godhavn; b-g from Egedesminde; h-l from holotype of *C. teres*: a, end of dorso-median radiole; b, c, dorsal and ventral staining pattern of anterior end of trunk; d, anterior view of third thoracic notopodium. Setae schematic, most upper limbate setae omitted from this segment; f, g, uncini from third and approximately 45th abdominal setigers; h, slightly schematic side view of anterior end, branchial crown omitted; i, end of fully developed radiole; j, spatulate seta from sixth setiger; k, l, abdominal uncini from third and approximately 70th abdominal setigers.

Broad notopodial lips in thorax. Spatulate setae with pointed tips. Abdominal uncini uniform, with straight crests; small crowns with some small teeth in several columns; rostra not extending beyond bases.

Material studied: Egedesminde and Godhavn, west coast of Greenland (SMNH 6861; 6862), and Safehavn and Hornsund, Spitsbergen (SMNH 6863; 6864 in part). The material of Malmgren (1866), 8 specimens.

Greenland, locality unknown. Collected by C. Lütken in the last century, USNM 372, 2 specimens.

Dutch Harbor, Alaska, holotype of *Chone teres*. PMNH 2761 (previous number: 5-2).

Additions to the Description: Since the type material from "the Greenlandic sea" is lost (letter by Dr. J. B. Kirkegaard, ZMC, 27 Feb. 1970), excellently preserved Arctic specimens of Malmgren (1866) are used for additions to the description of the species. The features of the especially suitable specimen from Egedesminde are stressed on the assumption that Kröyer's material was collected also off the west coast of Greenland where most of the traffic went during that time.

The trunks of the smallest specimens are a little less than 2 cm long, are about 1 mm wide, and have about 50 abdominal segments. Large specimens have 70 to 80 abdominal segments and are, when fixed in their tubes, up to 6 or 7 cm long (total) and about 3 mm wide. About 1½ cm of the length of the large animals is contributed by the branchial crown. The radioles number up to 15 or 16 pairs (up to 22 according to Kröyer, 1856). In addition to the radioles, about half a dozen pairs of inconspicuous nude ventral filaments are present; the longest ones are almost a fifth of the length of the branchial crown. The palmate membrane extends to two-thirds or three-quarters of the length of the radioles and continues as broad flanges on the radioles. The ends of the radioles are broad and short (Figure 1a); however, the most ventral pinnated radioles have relatively longer nude tips which are twice as long as shown in the figure and sometimes have an additional short filiform end.

The collar extends dorsally to the end of the second setiger (Figure 1b). Thus the furrow separating the first and second setigers does not reach the fecal groove. This character is easily made out. On the ventral side (Figure 1c), the first (buccal) segment is not distinctly separated from the collar in unstained animals. The body is essentially rounded and entirely covered by glandular tissue, i.e., no ventral shields are present. The glandularization is conspicuous even in unstained specimens. The segments appear as biannulate in the thorax and through the 40th to 50th abdominal setiger which is most of the abdomen, by length. Dorsally in the thorax after the second setiger, the intrasegmental furrows bend posteriorly before joining the fecal groove. This seems characteristic for the species; Hofsommer (1913), however, stated that the furrows bend forward. The postsetal glandular ring on the second setiger, usually appearing in *C. infundibuliformis* as a sunken fine line, is present (contrary to Ushakov, 1955).

The first bundle of thoracic setae originates slightly dorsad to the level of the notosetae of the following segments. In these segments notopodial lips are conspicuous (Figure 1d) when not withdrawn. Limbate and spatulate thoracic setae were figured by Malmgren (1866, Plate 28, Figure 87B, B^1, B^2). Whereas Malmgren depicted spatulate setae with and without pointed tips, I have found only setae with pointed tips (Figure 1e; animals from the four localities of Malmgren's material); these, of course, are often broken off. In the juvenile specimens, the tips are relatively twice as long as shown here. Bayonet-type setae have already been observed by Fauvel (1927) for the species. The thoracic uncini are arranged in irregular double rows except in juveniles; therefore, the oldest (i.e., the dorsal) upper parts of the tori of the adults have only single rows. The abdominal uncini have beaks which do not extend beyond the bases of the uncini (Figures 1f and 1g; checked also at 80th setiger, about 10 segments before the pygidium). The tips of the accessory teeth lie on the continuation of the rostra. In the anterior segments, these teeth seem to be of uniform size,

whereas posteriorly one larger accessory tooth can sometimes be distinguished. Several columns of teeth are present both anteriorly and posteriorly. The long and short limbate abdominal neurosetae are much finer posteriorly than anteriorly.

When treated with methyl green, the thorax and the anterior part of the abdomen stain uniformly. This holds also for the first segment which is visible only ventrally (Figure 1c). The collar shows a variable pattern, not related to locality or size of specimens. It can be either almost fully stained—nearly as intensive as the trunk—or be almost devoid of stain-accepting cells so that the anterior border of the first setiger is indicated only by a midventral white line. The intrasegmental furrow on the first setiger can be weakly indicated or not visible. Stain-accepting cells (and hence, presumably, the glandularization of the body surface) are not fully developed in juveniles. The cells are present in conspicuous concentrations only along the inter- and intrasegmental furrows leaving free areas between them, especially dorsally in the thorax.

The holotype of *Chone teres* was inspected, and the following additions to the description may be made; slight differences from typical *C. infundibuliformis* will be pointed out. The common base of the branchiae is hidden below in the collar which is relatively large (Figure 1h). The collar ends dorsally at the posterior border of the second setiger. The radioles are of unequal length, as if some were regenerating. The longest ones have very broad ends (Figure 1i). Segments are clearly biannulate through approximately the 35th abdominal segment; posterior to this region, staining helps to recognize the intrasegmental furrows. The anterior border of the first setiger is visible only ventrally and laterally (Figure 1h). The intrasegmental furrow of this segment is indicated merely by yellowish color after staining of the animal with methyl green. The anterior border and the intrasegmental furrow of the second setiger do not reach the fecal groove. The glandular girdle is irregularly broadened laterally. On the following thoracic segments, the intrasegmental furrows bend rearward dorsad of the notosetae and the intersegmental furrows bend forward before joining the fecal groove.

The setal bundle of the first setiger is only slightly smaller than those of the following segments but is situated in a slightly more dorsal position than that of the second setiger. As already stated by Bush (1904), geniculate setae are present in the remaining segments; the spatulate setae have pointed tips (Figure 1j). Thoracic uncini are arranged in irregular double rows in some parapodia. Abdominal uncini are nearly identical anteriorly and posteriorly (Figures 1k and 1l). Their crests are almost straight (less so posteriorly). Several rows of small accessory teeth are arranged in several columns. The rostra do not surpass the bases of the uncini; the cavities below the rostra are not rounded in side view as in Greenlandic, *C. infundibuliformis* (Figure 1f).

Upon staining, the thorax does not accept the dye dorsally as readily as laterally and ventrally; similarly, the ventral epidermis of the abdomen retains the dye longer than that of the dorsal side. In the abdomen the tissues along the inter- and intrasegmental furrows stain more strongly than the fields between them so that most segments appear to bear three whitish rings rather than one, the intrasegmental furrow. Yet, I have the impression that the epidermis is fully glandularized.

Remarks: *Chone teres* is considered a synonym of *C. infundibuliformis* although the abdominal uncini are slightly different and the ventral side in *C. teres* accepts stain relatively more than the dorsal side. Noteworthy is the shortness of the branchial crown which contributes approximately one-fifth of total length in Greenlandic specimens preserved in their tubes, but one-eighth in *C. teres*. All other specific characters agree. When more material from Alaska becomes available, special attention should be paid to the mentioned deviating characters to check the justification of placing *C. teres* in synonymy.

The record of *C. teres* by Chlebovich (1961) is not included among the synonyms of *C. infundibuliformis* because he lists *C. cincta* Zachs, as described by Ushakov (1955), among his

synonyms. The figure of the tips of the radioles of *C. cincta* by Ushakov (1955, Figure 159 K) clearly shows a feature very different from *C. infundibuliformis;* it may be noted that Zachs (1933), while describing *C. cincta,* observed that the gills are like those of *C. infundibuliformis.*

The number of records for the long-known *C. infundibuliformis* is very large. Lists by McIntosh (1923), Pettibone (1954), and Hartman (1969) may be consulted, but it must be noted that most of the records cannot be evaluated under the viewpoints presented here without the specimens of the various authors. Therefore, the list of synonyms on p. 461 has been kept short.

Regarding the distribution and synonymy of *C. infundibuliformis* in the North Atlantic, McIntosh (1916) was the first to emphasize the difference between the abdominal uncini of Greenlandic specimens (very small accessory teeth, forming a straight line with the rostrum, cf. Figure 1f) and those of southern forms (teeth coarse, their tips lying on a convex line above the continuation of the rostrum similar to Figure 3g), thus implying that different forms are involved. Most European records of *C. infundibuliformis* will not be identifiable without the authentic material of the several species; confusion is possible with *C. fauveli, C. normani,* and *C. reayi,* all described by McIntosh, and *C. ungavana* Chamberlin. Fauvel (1927, p. 346) has already suggested that *C. reayi* may belong to *Jasmineira* Langerhans.

From the description alone, it is certain that most, if not all, of the material of Fauvel (1913, 1914) is not *C. infundibuliformis.* McIntosh (1916) even believed that Fauvel had before him *C. duneri,* which is very different from any of the species listed in the previous paragraph. All of Fauvel's drawings of abdominal uncini show coarse accessory teeth not found in *C. infundibuliformis* from Greenland. Also, Fauvel (1913) stated that the teeth in some specimens were arranged in one row only. Fauvel emphasized the variability within specimens of the abdominal uncini (as well as of the tips of the spatulate setae) for his material. The shape of abdominal uncini, however, does not vary in *C. infundibuliformis.* Similarly, Lukasch (1911, Plate 2, Figures 7 and 8) shows a conspicuous divergence of the form of the anterior and posterior abdominal uncini in material from the Kola Fjord; as shown, this does not occur in Greenlandic material. Also, drawings in Fauvel (1927) do not refer to typical *C. infundibuliformis.* Further, Hartman's (1944b, Plate 23, Figure 46) figure of an uncinus of *C. infundibuliformis* from the Swedish west coast resembles that of *C. fauveli*; according to Eliason (1962, see his remarks under *C. duneri*), true *C. infundibuliformis* is not found on that coast. Finally, uncini vaguely similar to those of *C. fauveli* have been drawn by Rioja and Lo Bianco (1931) for Iberic material identified as *C. infundibuliformis,* so that this record too is uncertain.

CHONE PAUCIBRANCHIATA (KRÖYER)

SABELLA PAUCIBRANCHIATA Kröyer, 1856, p. 22.

Material studied: Holotype, from Finmark, northern Norway (from label). ZMC.

The original description was based on a single specimen. The species has been regarded since Malmgren (1866) as a junior synonym of *Chone infundibuliformis* Kröyer. However, the holotype has ventral shields whereas *C. infundibuliformis* does not. The shields are especially visible after using methyl green; the thorax laterally does not stain. The synonymy of this old species cannot be given without a thorough redescription of other European forms: possibly, the species is indeterminable.

The mature specimen, with polygonal eggs of about 50 μ diameter, is small, having a trunk length of about 10 mm to which the branchial crown adds about 3.5 mm. The greatest width is slightly less than 1 mm. Approximately 45 abdominal setigers are present. As observed by Kröyer (1856), the animal has three pairs of branchia and some short nude filaments. The length of the palmate membrane, which is now torn, extended at least to one-third of that of the branchial crown but not more than two-thirds. The thoracic uncini are long-handled. The first bundle of setae originates slightly more dorsally than the notosetae of the second setiger,

but all limbate setae are broken off so that a complete redescription of *C. paucibranchiata* is not possible.

CHONE DUNERI MALMGREN

Figure 2a, b

CHONE DUNERI Malmgren, 1867, p. 225.- Hofsommer, 1913, p. 336.- Pettibone, 1954, p. 339.- Hartmann-Schröder, 1971, p. 517.
CHONE sp. I Banse, Hobson, and Nichols, 1968, p. 547.
CHONE BIMACULATA Banse and Nichols, 1968, p. 227.- Nichols, 1968, p. 61.
not *CHONE DUNERI*.- Pettibone, 1956, p. 577 (a *Euchone* sp., see Remarks).

Diagnosis: A *Chone* of intermediate size without ventral shields. Branchial basis somewhat higher than oblique collar. Up to about 10 pairs of radioles, connected for about two-thirds of length by palmate membrane, with narrow, very long free ends. First bundle of setae very small. Conspicuous notopodial lips in thorax. Spatulate setae with pointed tips. Abdominal uncini with broad bases and small accessory teeth.

Material studied: Point Barrow, northern Alaska, 5 miles offshore, 89 m, 6 Oct. 1949. Collected by G. E. McGinitie, identified by M. H. Pettibone (Pettibone, 1954). USNM 23633, 2 specimens.

Paratypes of *C. bimaculata*, from station 5 of Lie (1968, 3 May 1963). USNM 36280, 4 specimens.

West Sound, Orcas Island, Wash., approx. lat 48°36'N, long 112°57'W, 40 m, mud, July 1967. Collected by H. L. Sanders. 1 specimen. Unpublished record.

Additions to the Description: The longest complete specimens at hand, from Point Barrow, are 18 and 26 mm long. In all animals examined, the free ends of the radioles are one-quarter to one-third as long as the entire radioles, tending to be relatively longest on the dorsal side of the branchial crown. Ventrally, about four pairs of nude filaments are found; two pairs are almost as long as the branchial crown and at least some have cartilaginous axes. As described by Malmgren (1867, Plate 14, Figure 75), the collar barely conceals the peristomium so that the branchial base is fully visible. The first (buccal) segment is not clearly distinguishable from the collar in unstained animals. A postsetal girdle of glands is present on the second setiger. Ventral shields are absent. The first fascicle of setae is very small in comparison with the following ones. From the second setiger on, notopodial lips are conspicuous. The thoracic neurosetae are winged hooks in Arctic and Puget Sound specimens (see Banse and Nichols, 1968, Figure 2g). An anterior abdominal uncinus is shown in Figure 2a.

The staining pattern of the specimens from Point Barrow (Figure 2b) is similar to that described by Hofsommer (1913) for an animal from the North Sea. In contrast to the appearance in species with ventral shields, the intensity and appearance of stained tissue in *C. duneri* is uniform around the entire circumference of the thorax and anterior abdomen. Ventrally, the small, weakly dyed fields in the presetal and postsetal rings are present also in the first abdominal setigers but disappear gradually by about the tenth abdominal segment. The dorsal pattern is characterized as follows: The median folds of the collar remain white. The unstained rings in the plane of the parapodia bend rearward on the dorsal surface similarly to but less pronounced than in *C. infundibuliformis* (Figure 1b). Weakly stained fields are present within the presetal stained rings of the thorax (cf. Hofsommer, 1913, text figure h); they extend laterally on the abdomen to the level of the neuropodia. Consequently the presetal rings of the anterior abdomen are nearly split in two. Occasionally, the postsetal rings are equally split but this is a condition which may occur also in other species without it having been noted herein. In most of the specimens from Washington which are smaller and in part not as well preserved, the pattern agrees but in some the dark longitudinal midventral strip is less conspicuous than in Figure 2b.

Remarks: Earlier authors have apparently not noted the glandular ring on the second tho-

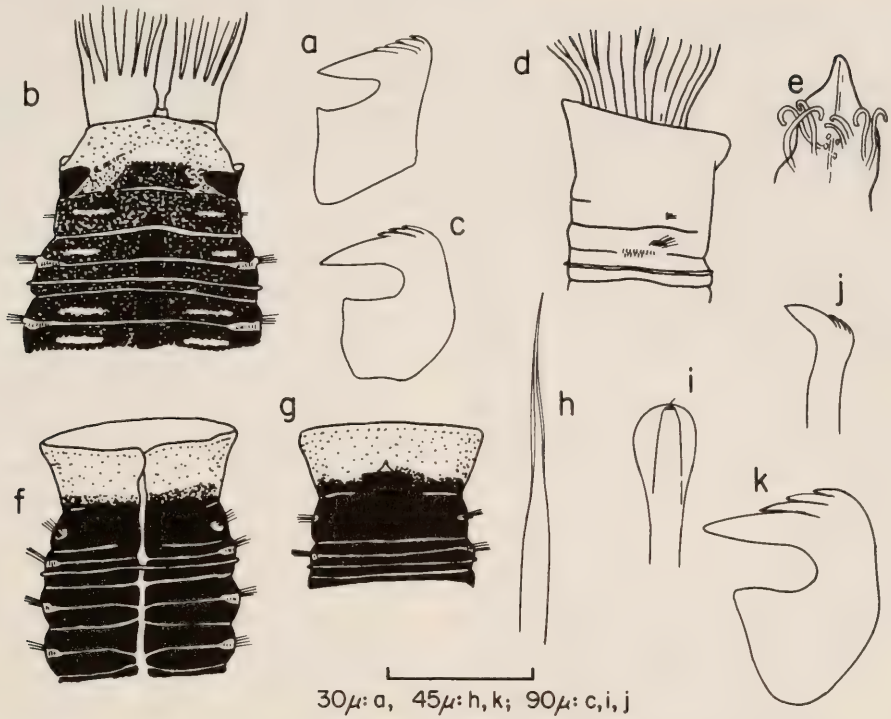

FIGURE 2.—*Chone duneri*, from Point Barrow: a, middle uncinus from fourth abdominal setiger; b, ventral view of anterior end of thorax after staining; *C. aurantiaca*; c from holotype, others from USNM 43637: c, uncinus from second abdominal setiger; d, anterior end from the right side; e, end of median radiole, somewhat schematic; f, g, anterior end in dorsal and ventral views after staining. Slightly schematic, branchial crown omitted; h, i, bayonet and spatulate setae from sixth setiger; j, uncinus from fourth setiger; k, uncinus from approximately 60th (12th to last) abdominal setiger.

racic setiger; Ushakov (1955) has specifically stated that it is absent. This character was one of the main reasons for describing *C. bimaculata;* at that time it was not realized that all *Chone* species have such a ring. Contrary to the original description, the intersegmental furrows of the paratype do not stain and the thoracic intrasegmental furrows, in the plane of the parapodia, are ventrally interrupted by the strongly stained longitudinal midventral line (cf. Banse and Nichols, 1968, Figure 2j). Thus, there is no justification for maintaining *C. bimaculata.*

The record of *C. duneri* from Labrador (Pettibone, 1956, USNM 23635, 2 specimens) is a *Euchone* sp. with conspicuous ventral shields.

CHONE AURANTIACA (JOHNSON)

Figure 2c-k

MEGACHONE AURANTIACA Johnson, 1901, p. 430.- Hartman, 1938, p. 19; 1959, p. 549.

Diagnosis: A large *Chone* species without ventral shields. Branchal basis shorter than the slightly oblique collar. About 25 pairs of radioles connected for four-fifths of length by palmate membrane, with free ends short and tapered. First bundle of setae small, inserted at same level as following notosetae. Spatulate setae without pointed tips. Abdominal uncini uniform, with a few columns of three to four coarse

accessory teeth each; rostra extending beyond bases. With caudal appendix?

Material studied: Holotype, from Port Orchard, Wash. MCZ 1933.

Near Friday Harbor, Wash., lat 48°31.7'N, long 122°58.0'W, at the 0-ft level, in shell gravel, 6 July 1953. Collected and identified as *C. infundibuliformis* by R. I. Smith. FHL 1700, 1 specimen. Unpublished record.

From same site, presumably intertidal, in fine gravel, 10 July 1968. Collected by S. Heller. USNM 43637, 1 specimen. Unpublished record.

Redescription: The holotype is now very poorly preserved; it apparently had been allowed to become dry. The diagnostic characters, i.e., the position of the setae on the first setiger, the form of the spatulate setae (in one notopodium), and the abdominal uncini (Figure 2c) can still be recognized; the collar has been depicted by Johnson (1901, Plate 18, Figure 186). According to Johnson, the trunk had 75 setigers and was 87 mm long.

The following description is based on the two animals from near Friday Harbor which are complete, fixed outside their tubes, and well preserved. One specimen (USNM) has 8 thoracic and almost 70 abdominal setigers. The length of the branchial crown is approximately 10 mm, that of the trunk roughly 60 mm, and the greatest width is about 3 mm. The other animal (FHL) has approximately 60 abdominal setigers, its trunk length is about 60 mm, the greatest width almost 5 mm, and the branchial crown approaches 15 mm in length.

In the preserved material the branchial crown forms a funnel with reflexed upper margin, as common in the genus. The basis of the crown is hidden by the collar (Figure 2d). The number of radioles is 20 pairs (USNM) and 26 pairs (FHL). They are united by a palmate membrane for about four-fifths of their length. The tips of the radioles extend beyond the origin of the distal pinnules; they are short and broad, tapering at the ends (Figure 2e). Ventrally the tips are slimmer, dorsally a little wider than shown. Many pinnules reach almost to the ends of the radioles. As nude filaments were not found, they must be very short. The palps are small triangular processes.

The collar is slightly oblique, being a little longer ventrally than dorsally. It extends dorsally to the intrasegmental furrow of the second setiger (Figure 2f). Consequently, the posterior border of the first setiger does not end in the fecal groove. Ventrally, the first (buccal) segment is not clearly set off from the collar. Ventral shields are not present, and the entire epidermis is glandularized. Setigers in the thorax and abdomen are biannulate. The intrasegmental division of the first setiger is poorly discernible and has not been drawn in Figure 2g. The dorsal pattern of the inter- and intrasegmental borders in the thorax is shown in Figure 2f. The pygidium is pointed. A damaged filiform appendage was seen in one specimen (USNM). It appears to be similar to the caudal appendage of *C. filicaudata* Southern. It is absent in the other animal (FHL).

The first setiger has bundles of a few short setae which insert at right angles to the notosetae of the following segments but on the same level (Figure 2d). Each of the remaining thoracic notopodia has almost 2 doz of upper limbate setae in two sizes and below an anterior series of bayonet-type setae (Figure 2h) with shafts almost as thick as the posterior series of spatulate setae; the bayonet-type setae taper abruptly at about the level of the body surface. The spatulate setae (Figure 2i), 1½ to 2 doz per parapodium, are without pointed tips but some have very tiny hairs instead. The distal end of such a seta can appear as having a dimple. These spatulate setae are present also in the holotype, but were overlooked by Johnson (1901).

About 3 doz of neuropodial hooks (Figure 2j) are arranged in irregular double rows in most thoracic neuropodia. The uppermost half dozen or so are in single rows. The abdominal uncini (Figure 2k) are uniform in shape anteriorly and posteriorly. When seen from the side, they have three or four large coarse accessory teeth arranged in three or four columns. The rostra extend beyond the bases. Two dozen uncini are present even in the 50th to 60th setigers.

Some irregular orange-red speckles remain on the collar and anterior segments of the holotype

which was preserved in Formalin and stored in alcohol. The second specimen was orange-red in life as was the holotype while freshly preserved (Johnson, 1901). Upon staining with methyl green the entire body surface turns uniformly green except for the collar and the inter- and intrasegmental furrows.

Remarks: Because of the presence of spatulate setae in the type species, *Megachone* is a synonym of *Chone* (cf. p. 461).

Megachone aurantiaca may be distinguished from the similar species, *C. infundibuliformis*, by the insertion of the first thoracic bundle of setae and the form of the abdominal uncini. *Chone magna*, when deprived of the branchial crown, will also be difficult to distinguish from *C. aurantiaca* but can be recognized by the same diagnostic characters. *Chone mollis*, the third fairly large species of *Chone* on the North American west coast, has a different arrangement of intersegmental furrows anteriorly (Figure 3c), large notopodial lips and somewhat different abdominal uncini, especially posteriorly (Figure 3h).

CHONE MOLLIS (BUSH)

Figure 3

METACHONE MOLLIS Bush, 1904, p. 216.
CHONE MOLLIS.- Hartman, 1942b, p. 87; 1944b, p. 279; 1969, p. 673.

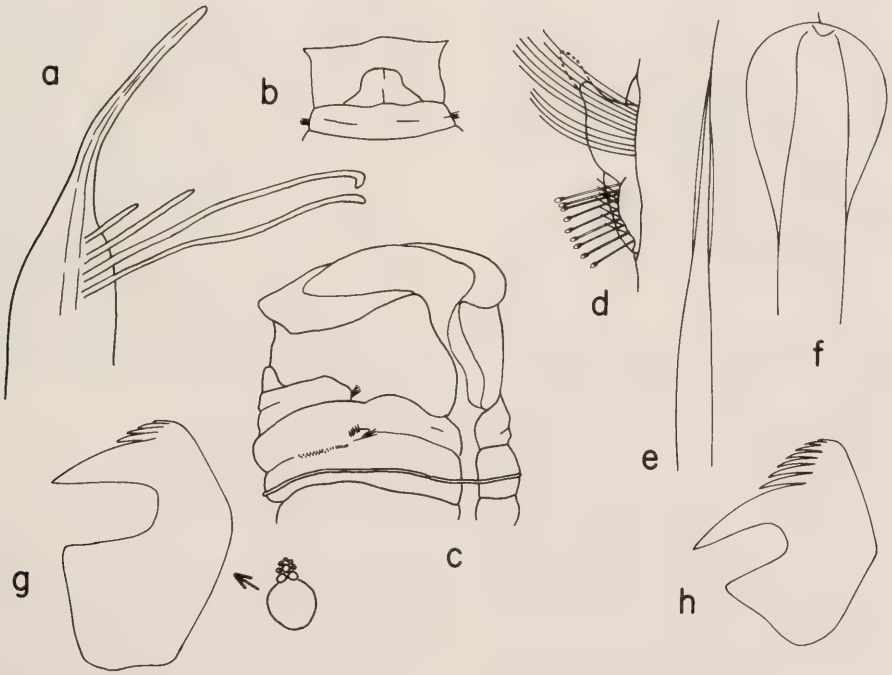

FIGURE 3.—*Chone mollis*; AHF 003258, setae not drawn to scale: a, end of median radiole, pinnules schematically drawn for one side; b, ventral view of anterior end. Somewhat schematic, branchial crown omitted; c, anterior end from the right side, branchial crown omitted; d, anterior view of thoracic notopodium. In dotted outline the extended cirrus; e, bayonet-type seta; f, spatulate seta; g, uncinus from second abdominal setiger. Detail: top viewed *en face;* h, uncinus from 30th abdominal setiger (of about 40 total abdominal segments).

Diagnosis: A large *Chone* species without ventral shields. Branchial basis hidden by level collar. Approximately 15 pairs of radioles connected for two-thirds of length by palmate membrane, with free filiform ends of intermediate length. First bundle of setae small, inserted in a furrow (continuation of anterior border of first setiger) on same level as following notosetae. Conspicuous notocirri and notopodial lips in thorax. Spatulate setae without pointed tips. Anterior abdominal uncini with rostra about as long as bases, few coarse teeth in two columns; crowns somewhat enlarged in posterior segments.

Material studied: Tomales Bay, Calif., near the low tide line. Summer 1941. Collected by F. A. Pitelka; identified by O. Hartman. AHF n 424, 2 specimens.

Tomales Bay, Calif., clam flats. 8 June 1941. Collected by S. F. Light; identified by O. Hartman. AHF 003258, 2 specimens.

Off Long Beach, Calif., *Velero* station 4886, lat 32°42′34″N, long 118°08′15″W, 22 Feb. 1957. AHF 003218, 6 specimens.

Inner Tomales Bay, Calif., across from the village of Marconi. Coarse intertidal sand. Collected and identified by J. S. Tucker. 6 specimens.

Additions to the Description: The largest animals (AHF 003258) are up to 5 cm long (total) and 3 mm wide. The ends of their radioles have flanges (Figure 3a) that taper fairly abruptly at the level of the last pinnules. In specimens from Tomales Bay of 3-cm length and 2-mm width, the free ends may be almost twice as long as shown in the figure. The largest of the several ventral nude filaments recognizable in the latter specimens reach two-thirds of the length of the branchial crown.

The anterior end is distinguished ventrally by a very prominent first (buccal) segment (Figure 3b) that is clearly set off from the collar and tends to be split longitudinally. The anterior border of the first setiger is complete; laterally, it converges with the anterior border of the second setiger where the first bundle of setae inserts (Figure 3c). The furrow between the first and the second setiger extends to the fecal groove. The segments may appear as biannulate at least through the 25th abdominal setiger.

The thoracic notopodia (Figure 3d) have massive lips. The posterior lips bear more or less contracted notocirri. The whole structure may be almost completely withdrawn into the surrounding epidermal pocket so that only the contracted cirrus, resembling a papilla, is visible under favorable illumination. The bayonet-type setae (Figure 3e) arise from the anterior lower lip shown in Figure 3d. The diameter of their shafts is three-fourths the width of the spatulate setae. They taper abruptly at about the level of the body surface. Spatulate setae (described by Hartman, 1944b, as having a dimple) sometimes have very minute tips (Figure 3f) which presumably are usually broken off. Thoracic uncini may or may not be arranged in irregular double rows. The anterior abdominal uncini (Figure 3g; cf. Bush, 1904, Plate 35, Figure 28; Hartman, 1942b, Figure 141; 1944b, Plate 23, Figure 49) have small and few teeth, in two columns. Posteriorly, however, the number of rows increases (Figure 3h) as well as the number of columns.

In stained specimens, the entire epidermis is uniformly green, i.e., ventral shields are absent. A white crescent-shaped area is found ventrally on the collar anterior to the first segment. The intrasegmental furrows, dorsally in the thorax, are inclined rearwards as in *C. magna* (cf. Figure 5e).

CHONE GRACILIS MOORE

Figure 4

CHONE GRACILIS Moore, 1906, p. 257.- ?Hartman, 1961, p. 42; 1969, p. 665 (same record).
not *CHONE GRACILIS* Moore.- Berkeley and Berkeley, 1932, p. 315; 1942, p. 206; 1952, p. 123, in part (for all, see *C. ecaudata*).
not *CHONE GRACILIS* Hofsommer, 1913, p. 342 (homonym).
CHONE INFUNDIBULIFORMIS.- Pettibone, 1954, p. 378, in part.

Diagnosis: A *Chone* species of intermediate size without ventral shields. Ten pairs of ra-

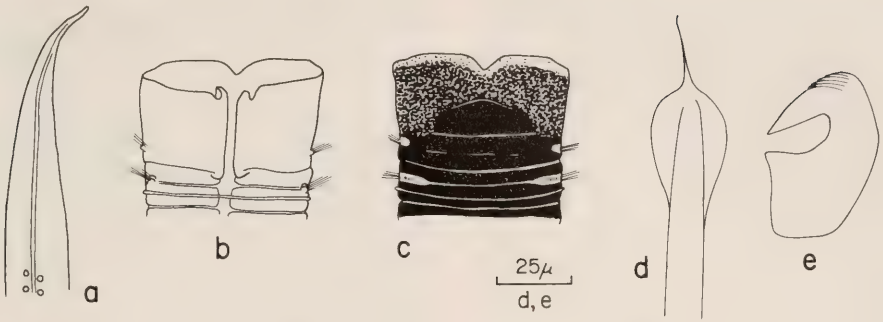

FIGURE 4.—*Chone gracilis*, from holotype: a, end of median radiole. Origin of pinnules indicated schematically; b, dorsal view of anterior end, branchial crown omitted; c, ventral staining pattern of anterior end of trunk; d, spatulate seta from sixth setiger; e, uncinus from third abdominal setiger.

dioles connected for three-fifths of length by palmate membrane, with free ends gradually tapering to pointed tips. Branchial basis as high as collar; collar almost level, with distinct ventral indentation. First bundle of setae of normal size, inserted at same level as following notosetae. Rounded notopodial lips in thorax. Spatulate setae with long pointed tips. Abdominal uncini uniform, with small accessory teeth in several columns; rostra not extended beyond bases.

Material studied: Holotype, from Kodiak Island (originally spelled Kadiak), southwestern Alaska. USNM 5513.

Additions to the Description: The original description of the specimen, a mature female, was rather complete but was accompanied only by a few figures so that there has been some confusion with other species. The branchial basis is as high as the collar. A tip of a median (lateral) radiole is shown in Figure 4a. The collar (Figures 4b and 4c) inserts dorsally on the anterior part of the second setiger. The free dorsal edge of the collar is folded inwards as stated by Moore (1906). The edge rises ventrolaterally and ventrally slightly over the height attained dorsally. A midventral indentation of the collar is very conspicuous. The first (buccal) segment is distinct ventrally even without staining. The intrasegmental furrow on the second setiger reaches the fecal furrow. A postsetal girdle of glands is present on this setiger. The first bundle of setae, now preserved on only one side, is of ordinary relative size and inserts at the same level as the notopodia of the following segments. Moore (1906, Plate 12, Figure 62) depicted bayonet-type setae without designating them as such. The spatulate setae (Figure 4d) have unusually long tips as shown also by Moore (1906, Plate 12, Figure 64). The abdominal uncini (Figure 4e) are uniform throughout and have about six rows of approximately six small teeth which are difficult to count. Upon staining with methyl green, thorax and most of the abdomen turn uniformly green excepting the intersegmental and intrasegmental furrows; also, the presetal parts of the segments dorsal in the thorax are paler than the postsetal parts. Ventrally, the incomplete anterior and posterior borders of the first segment are distinct. The intrasegmental furrow of the first setigerous segment is poorly visible.

Remarks: I concur with Moore (1906) that this is a species of its own; it is distinct from *C. infundibuliformis* (contrary to Pettibone 1954). Based on his description and the observations provided here, *C. gracilis* is distinguished among the species with glandularized epidermis by its ventrally indented collar; another diagnostic character is the combination of a relatively long branchial crown which contributes more

than one-third of the total length, with the form of the tips of the radioles and spatulate setae, the insertion of the collar dorsal on the second setiger, and the form of the abdominal uncini.

The species is definitely known from southwestern Alaska. Hartman (1961, 1969) recorded it from California but referred expressly to the description by Berkeley and Berkeley (1952). As this largely represents *C. ecaudata* (see p. 473), the record needs confirmation.

CHONE MAGNA (MOORE)

Figure 5

EUCHONE MAGNA Moore, 1923, p. 245.- Hartman, 1961, p. 42.

CHONE MAGNA.- Hartman, 1969, p. 669.

Diagnosis: A large *Chone* species without ventral shields. Branchial basis shorter than oblique collar. About 30 pairs of radioles, connected for two-thirds of their length by palmate membrane, with free ends narrow and very long. First bundle of thoracic setae small, inserted slightly ventrad to following notsetae. Spatulate seta without pointed tips. Abdominal uncini uniform, with three of four coarse accessory teeth in two columns; rostra extending beyond bases.

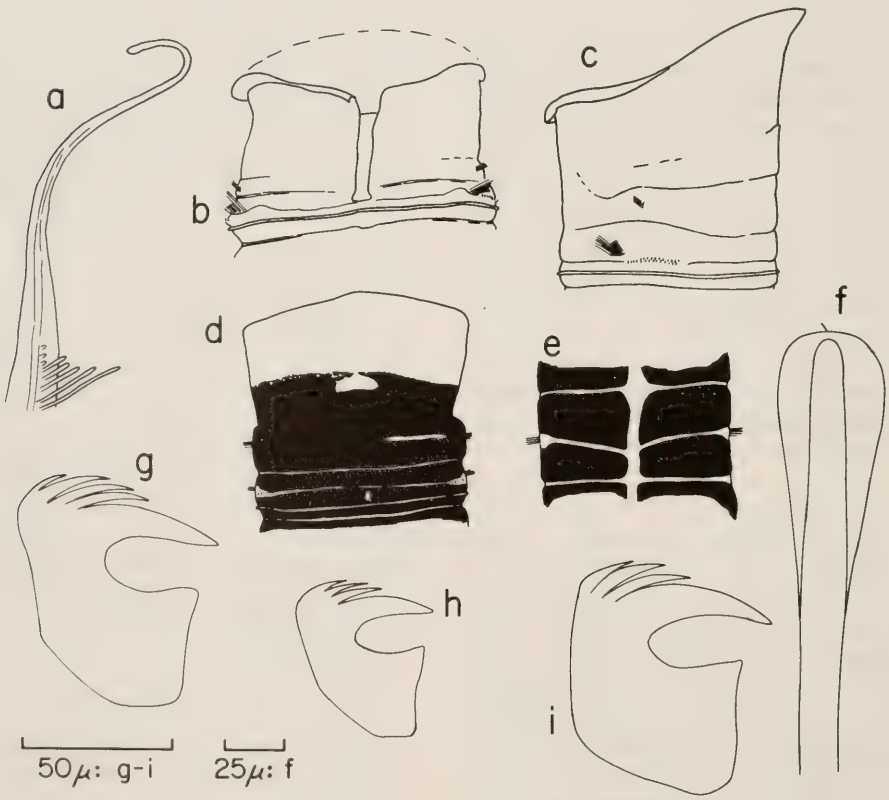

FIGURE 5.—*Chone magna*; e, g, and h from holotype, the others from animals from Washington: a, end of radiole; b, c, ventral and side views of anterior end, branchial crown omitted, setae schematic; d, ventral view of anterior end of stained specimen, body outline schematic; e, dorsal view of posterior thoracic segment of stained specimen; f, spatulate seta; g, h, uncini from 30th and approximately 70th (last of fragment) abdominal segments; i, uncinus from 70th (10th before last) abdominal segments from other animal.

Material studied: Holotype, from almost 500-m depth off California. USNM 17281.

North of Santa Catalina Island, Calif., *Velero* station 1178, between lat 33°30′45″N, long 118° 30′40″W, and lat 33°27′40″N, long 118°30′00″W, 72 to 78 m, sand, 10 Sept. 1940. Identified by O. Hartman. AHF 003259, 1 specimen.

Off Upright Head, Lopez Island, Wash., approx. lat 48°35.5′N, long 122°53′W, 2 Aug. 1960. Collected by R. P. Dales and G. John. FHL 293, 1 specimen. New record.

South of Orcas Island, Wash., lat 48°34.9′N, long 122°50.8′W, 40 to 54 m, 13 Aug. 1964. Collected by S. van Niel. USNM 43636, 1 specimen. New record.

Additions to the Description: The two large complete animals from the San Juan Islands, Wash., were compared with the holotype. The slightly larger one (FHL) has about 65 abdominal setigers and is approximately 7.5 cm long (total) and 0.5 cm wide. The trunk of the Californian specimen (AHF) is slightly longer than 2.5 cm.

The branchial crown, previously unknown, contributes about one-fourth of the total length. The larger specimen has 30 pairs of radioles; in addition, about six pairs of nude filaments maximally one-fifth as long as the branchial crown are present. The palmate membrane connects three-fifths of the length of the radioles. Their free ends (Figure 5a) are 3 to 5 mm long and sometimes coiled up like a watch spring. The very numerous pinnules are about 1.5 mm long.

The collar (Figures 5b and 5c), well recognizable also in the holotype, is large for a species of *Chone*, markedly higher ventrally than dorsally and often opened and folded backward. When closed, it probably conceals fully the common basis of the radioles. The dorsal slit extends to the middle of the second setiger (Figure 5b). The first setiger is indistinctly set off from the first segment; the border is morphologically visible but is not indicated by a white line after staining (Figures 5c and 5d). The setae on the first setiger arise in a more ventral position than the notosetae on the following segments (Figure 5c).

Additions to Moore's description of the trunk are the following: A glandular postsetal girdle is present on the second setiger. The intrasegmental furrows in the middle and posterior thorax are not parallel to the intersegmental furrows (Figure 5e). Ventral shields are absent, i.e., the epidermis is completely glandularized and stains uniformly in the thorax and most of the abdomen, except for the inter- and intrasegmental furrows (Figure 5d).

Bayonet-type setae are present. The spatulate setae of the holotype, (stated by Moore, 1923, to be without a mucron) are lost and those of the Californian specimen are damaged. The spatulate setae of the material from Washington have hairs on their tips (Figure 5f). The thoracic uncini tend to be arranged in irregular double rows in the large animals. Anterior and posterior abdominal uncini (Figures 5g-i) have beaks longer than the bases, with three or four coarse accessory teeth above them. In frontal view, the teeth appear to be in a single row in most cases; occasionally I have seen two side by side. The difference in outline between Figures 5h and 5i is probably more a question of orientation than real.

Remarks: *Euchone magna* was transferred to *Chone* by Hartman (1969). It seems likely that Moore (1923) placed the species in *Euchone* due to a mistake while reconstructing his lost manuscript of 1911: His text states clearly the absence of a caudal membrane. Also, the vial contains a provisional label, *Chone magna*, which is written on stationery of the Philadelphia Academy and, according to Dr. M. H. Pettibone, is in Moore's handwriting.

The species has been known previously only from California.

CHONE ECAUDATA (MOORE)

Figure 6

JASMINIERA ECAUDATA Moore, 1923, p. 246.

CHONE ECAUDATA.- Hartman, 1942a, p. 135; 1969, p. 663.- Berkeley and Berkeley, 1950, p. 67; 1952, p. 124.

CHONE GRACILIS.- Berkeley and Berkeley, 1932, p. 315; 1942, p. 206; 1952, p. 123, in part.

CHONE MINUTA Hartman, 1944b, p. 280; 1969, p. 671.- Rioja, 1963, p. 218.
?*CHONE TERES*.- Okuda, 1934, p. 236; 1946, p. 171.- Imajima and Hartman, 1964, p. 365.

Diagnosis: A small *Chone* species with ventral shields. Six to eight radioles connected for approximately one-half of length by palmate membrane, with free ends of variable length. Collar low, almost level, barely covering the branchial basis, with overlapping dorsal ends. First bundle of setae large, on same level as following notosetae. Conspicuous rounded notopodial lips in thorax. Spatulate setae with long pointed tips. Anterior abdominal uncini with rostra longer than bases, with several rows of teeth in several columns; crowns posteriorly much higher, bases rounded.

Material studied: Two syntypes from off Santa Cruz, Calif. Dr. M. H. Pettibone (personal communication) suggested that following Moore's handwritten label, the smaller, complete specimen should be designated the holotype. USNM 17319.

Dillon Beach, Calif., July 1933. Collected by O. L. Williams; originally identified as *C. minuta*. AHF 003229, 11 specimens of a larger sample.

Fort Bragg, Calif., abundant in tunicate and *Lissodendoryx* colonies and eel grass, 29 June

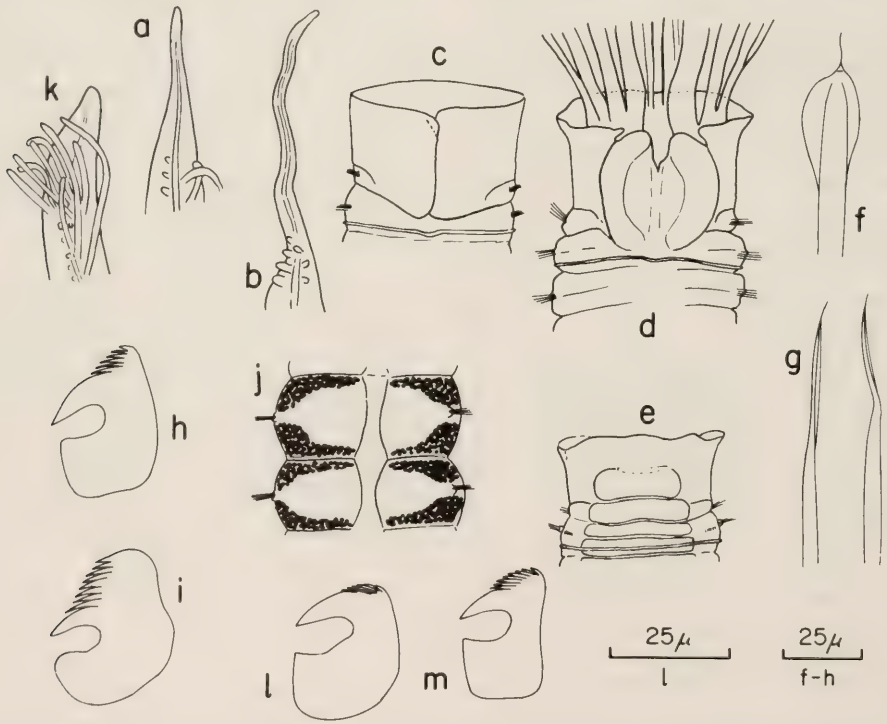

FIGURE 6.—*Chone ecaudata*; a-c, f from types d, e, and k from USNM 40304, h, i from AHF 2720, g, j from AHF 2721, l, m from USNM 45267: a, b, ends of dorso-lateral and ventralmost radioles; c, dorsal view of anterior end, branchial crown omitted (paratype); d, same view, with opened collar; e, ventral view of anterior end of specimen in Figure d; f, spatulate seta from third setiger; g, bayonet-type setae; h, i, largest and smallest uncini from 18th abdominal setiger (out of 25 total). Figure i is enlarged twice over Figure h; j, dorsal staining pattern in midthorax; k, end of lateral radiole; l, uncinus from third abdominal setiger; m, uncinus from 28th abdominal setiger, 20 μ high.

1934. Originally identified as *C. minuta*. AHF 003230, 5 specimens of a larger sample.

Holotype of *C. minuta* from Dillon Beach, Calif., in holdfasts of algae and among compound ascidians, 14 June 1941. AHF n 417; type AHF-67, Poly. 0182.

Wreck Bay, British Columbia, 1921 (see Berkeley and Berkeley, 1932, as *C. gracilis*). USNM 40722, 16 specimens.

Wreck Bay, west coast of Vancouver Island, 1925. Collected and identified by E. and C. Berkeley (see Berkeley and Berkeley, 1950). USNM 40303, 2 specimens.

Horsewell Point, British Columbia, in seaweed, 25 Apr. 1934. Collected by E. and C. Berkeley and identified as *C. gracilis*. USNM 40721, 2 specimens. Unpublished record.

Dodd's Narrows, British Columbia, 19 June 1957. Collected and identified by E. and C. Berkeley. USNM 40304, 1 specimen. Unpublished record.

Pavlov Bay, Alaska (see Berkeley and Berkeley, 1942, as *C. gracilis*). USNM 40723, 3 specimens.

Samami, Hokkaido, Japan, Aug. 1970. Collected by M. Imajima and identified as *C. teres*. USNM 45267, 3 specimens out of a much larger original sample.

Additions to the Description: The syntypes of *C. ecaudata* are mature females. The complete holotype has 18 abdominal setigers and is about 9 mm long (total); the paratype is a larger anterior fragment which is almost twice as wide.

A palmate membrane that "extends well over half the length of the radioles" (cf. Hartman, 1942a, p. 136) connects seven pairs of radioles bearing pinnules. A few pairs of nude filaments are present ventrally, the longest being almost half as long as the radioles proper. The ends of the radioles beyond the origin of the distal pinules are rather short dorsally (cf. Figure 6a). Laterally and ventrally, the ends can be "coiled like a watch spring" (cf. Moore, 1923, p. 246), having long filiform tips and being about a quarter as long as the entire radioles. A ventral radiole may be present, as long as the others but with an especially long terminal portion, the pinnules not extending as far as on the other radioles (Figure 6b; in one of the types, and USNM 40304).

The low collar barely conceals the bases of the branchial crown. When closed, it overlaps dorsally (Figure 6c); when open as in the holotype, it is formed as shown in Figure 6d (from another specimen; the outer heavy lines in this figure correspond to the edges of the collar in Figure 6c; the anterior incision extends almost to the level of the first bundle of setae in the holotype of *C. minuta*).

Ventral shields and intrasegmental furrows are more or less visible depending on the contraction of the animals (Figure 6e). After weak staining, however, the ventral shields and the biannulated character of the setigers are very distinct as far as the middle of the abdomen in all animals.

The first (buccal) segment (Figure 6e) is unusually large and distinct ventrally. The anterior border of the first setiger approaches the posterior border dorsad to the setae (Figures 6c and 6d). This bundle of setae is as large as those of the following notopodia and emerges on the same level. Rounded anterior and posterior notopodial lips are conspicuous. The limbate setae originate above the lips. All specimens have spatulate setae with long tips (Figure 6f). Bayonet-type setae, with shafts of the same diameter as the spatulate setae, are also present (Figure 6g). A thoracic uncinus of the holotype of *C. ecaudata* was figured by Hartman (1942a, Figure 15g). Other Californian material seems to have uncini with slight wings (Hartman, 1944b, Plate 23, Figure 51) as I have observed for a specimen from British Columbia (USNM 40304). Hartman (1942a, Figure 15f) depicted two abdominal uncini from anterior segments. No satisfactory view of posterior abdominal uncini was obtained from the type material. Anterior and posterior abdominal uncini differ in other California specimens. Anteriorly, four or five rows of accessory teeth in six to eight columns are situated above the rostrum; the rostrum extends beyond the basis (cf. Figure 6h; also Hartman, 1944b, Plate 23, Figure 50). Posteriorly, some uncini having the same shape occur in the same tori with smaller

ones that have higher crowns and more rounded bases (Figure 6i).

After staining of the types of *C. ecaudata*, the ventral shields in the thorax and abdomen are darkest, except for a small area on the anterior border of the first segment (cf. Figure 6e). Most parts of the collar, except for the anterior edge, are stained in the types but may be whitish in other specimens. Dark areas around the thoracic parapodia are separated from the shields by a spottily stained longitudinal band. This is especially obvious in specimens from British Columbia. In some of the other Californian animals (AHF 003230), the thorax seems to stain similarly laterally and ventrally under low power, but when viewed under 100 ×, the lateral areas appear in a granulated pattern, in contrast to the uniformly stained ventral region.

The dorsal pattern, beginning in the middle thoracic segments (Figure 6j), is present in all animals and seems to be very characteristic. It results from the widening of the nonstaining epidermis of the intrasegmental furrow. This pattern continues on the anterior abdominal setigers, but the unstained areas become progressively narrower until, in the middle part of the abdomen, the pale intrasegmental lines are as narrow as the intersegmental rings. In some Californian specimens (AHF, originally identified as *C. minuta*), a conspicuous subcircular spot of heavily stained cells straddles each intersegmental furrow at the level of the parapodia in the posterior thoracic and anterior abdominal segments. The staining pattern was not studied in the holotype of *C. minuta*.

The variability of the ends of the radioles is noteworthy; their shape is not related to size or the region where collected. In material from British Columbia (USNM 40303, 40304), a complete mature female, 11 mm long and 0.9 mm wide, has six pairs of radioles connected for two-thirds of their length by the palmate membrane. The free ends of the radioles scarcely extend beyond the ends of the pinnules (Figure 6k). Also within the samples from California, the length of the free ends of the lateral radioles is variable, sometimes being intermediate between that shown in Figures 6a and 6b, or is even shorter (cf. Hartman, 1944b, Plate 24, Figure 59). The Californian specimens (AHF), some of which are mature, are up to 15 mm long, and have up to 29 abdominal setigers and seven or eight pairs of radioles (usually connected for half of their length). Although in other species of *Chone* the width of the flanges (i.e., the extension of the palmate membrane) varies between the dorsal- and ventralmost radioles such that the ventral ones appear slimmer, the relative length of the free part is usually fairly consistent (see, however, *C. infundibuliformis*, p. 462).

Remarks: *Chone minuta* agrees with *C. ecaudata* by its size, the shape of the collar, the fairly distinct ventral shields, the form of the spatulate setae and anterior abdominal uncini, and the dorsal staining pattern in the thorax (the last character was not checked in the holotype of *C. minuta*). The variability in the length of the free ends of the radioles of the specimens originally described as *C. minuta* is notable.

Among the material identified by the Berkeleys as *C. gracilis*, the lot from Horsewell Point (USNM 40721) allowed staining; the pattern, in addition to the form of the branchial crown, the collar, the ventral shields, and the form of the spatulate setae make identification certain. The lot from Wreck Bay (USNM 40722) is referred here with some hesitation because of the bad preservation. The branchial crown, ventral shields, and the form of spatulate setae, however, agree with *C. ecaudata*. Berkeley and Berkeley had recorded *C. ecaudata* from Wreck Bay in 1950.

With considerable hesitation, Japanese material from Hokkaido, originally identified by Dr. M. Imajima as *C. teres*, is included here. These specimens correspond closely to the description of *C. teres* by Okuda (1934), which, however, does not refer to *C. infundibuliformis* (cf. p. 461). The collars are of even height ventrally and laterally but are lowered dorsally, which is not the case in typical *C. ecaudata* (cf. Okuda, 1934, Figure 3). The radioles end as shown in Figures 6a and 6k. The uncini from anterior segments differ considerably from those in posterior segments (Figures 6l and 6m). The staining pattern dorsally in the thorax is similar to that of *C. ecaudata* (Figure 6j) except that the

pigment-free areas in the middle of the segments are narrower. The main difference between the specimens from Hokkaido and typical *C. ecaudata* is the apparent absence of ventral shields, both morphologically and in fully stained specimens; the distribution of stain-absorbing cells seems to be uniform ventrally of the setae. In animals where the dye has almost been differentiated, however, one does see stronger staining ventrally, and the indication of a whitish line ventral to the parapodia. The Japanese animals are included in *C. ecaudata*, in spite of the fact that the ventral shields seem to be almost absent, because of the general agreement with the typical form and because of the transitional character of specimens from Alaska (USNM 40723). Here, the collar is formed as in Japanese material, but morphologically distinct shields are present. Staining was not possible. Evidently, additional collections are needed for the study of the Alaskan and northwest Pacific forms. The record of *C. teres* by Uchida (1968) cannot be identified from the brief description.

CHONE ENIWETOKENSIS (REISH) NEW COMBINATION

EUCHONE ENIWETOKENSIS Reish, 1968, p. 225.

Material studied: Holotype (USNM 38406) and paratype (USNM 38407), from the Marshall Islands.

Diagnosis: A very small *Chone* species with weakly developed ventral shields and 13 to 14 abdominal setigers. Three to four pairs of radioles connected by palmate membrane for one-third of length. Collar oblique. Subspatulate setae with very long pointed tips. Abdominal uncini uniform, with a few teeth; rostra larger than bases.

Additions to the Description: The collar is higher ventrally than dorsally and has a broad, midventral lowering of the anterior edge. The postsetal girdle of glands is present on the second thoracic setiger. The holotype, but not the paratype, has a similar but somewhat irregular ring also on the fifth setiger. The fifth setiger of the paratype does not appear to be damaged, although otherwise the paratype is somewhat macerated. The ventrum of the thorax stains strongly; however, ventral shields could not be distinguished morphologically. The posterior end is strongly compressed dorso-ventrally suggesting, in unstained material, an anal depression. Treatment with methyl green showed uninterrupted segmental rings of staining cells around the posterior ends.

Remarks: This species is referred to *Chone* because the posterior end lacks the anal depression typical of *Euchone*. The species is not yet well characterized; moreover, it is not known whether the specimens were fully grown. If the fifth thoracic setiger indeed carries a glandular ring, the species would be uniquely distinguished.

CHONE VELERONIS NEW SPECIES

Figure 7

Holotype: From *Velero* station 6104, lat 33°39′45″N, long 118°06′40″W, 26 m, dark gray silty fine sand, 19 Feb. 1959. AHF Poly. 0459.

Paratypes: Same station and date. AHF Poly. 0460 (>10 specimens).

Diagnosis: A small species of *Chone* without ventral shields, with a greatly broadened postsetal girdle of glands on second setiger. Branchial crown long, with very high basis and six to seven pairs of radioles with filiform free ends. Collar low. Palmate membrane reaching beyond distal pinnules. Spatulate setae with pointed tips. Anterior abdominal uncini markedly different within tori, largest with small teeth, rostra as long as bases; small uncini with greatly enlarged crown. Posterior uncini only of the latter kind.

The species is named after the present ship of the Allan Hancock Foundation, the *Velero IV*, which collected the specimens.

Material studied: About 10 specimens of the type series.

Description: Mature animals, with about 45 abdominal setigers, are 11 to 12 mm long, of which approximately 3 mm are contributed by the branchial crown, and 0.5 to 0.6 mm wide. The smallest animal at hand has about 35 abdominal setigers and is 5 mm long and 0.3 mm wide. All specimens are well preserved.

The branchial crown has six to seven pairs of radioles, on an unusually high basis (Figure 7a). The radioles are connected by a palmate membrane that extends beyond the origin of the distal pinnules (Figure 7b). The narrow free tips are one-eighth to one-sixth as long as the radioles. Nude filaments were not found.

The low collar usually does not conceal the anterior part of the first (buccal) segment fully; it is somewhat higher ventrally than laterally (Figure 7a and 7c) and entire, except for the dorsal slit which reaches to the intrasegmental furrow of the second setiger. The first segment is sometimes distinct ventrally (Figure 7a). The posterior border of the first setiger does not quite extend to the fecal groove. Segments, except the first one, are biannulate in the thorax and the anterior half of the abdomen. The thoracic intrasegmental furrows bend rearward similar to those of *C. magna* (cf. Figure 5e). The postsetal glandular girdle of the second setiger (Figure 7a) is ventrally greatly broadened, extending into the third setiger. Laterally it is narrowed but still broader than on the dorsal side where it is similar in width to that of other species of *Chone*. The girdle has the same shape in the smallest animal available. A longitudinal band of whitish glandular tissue extends midventrally from the girdle onto the collar. Similar tissue is present is rings near the anterior edges of the posterior thoracic and about half of the

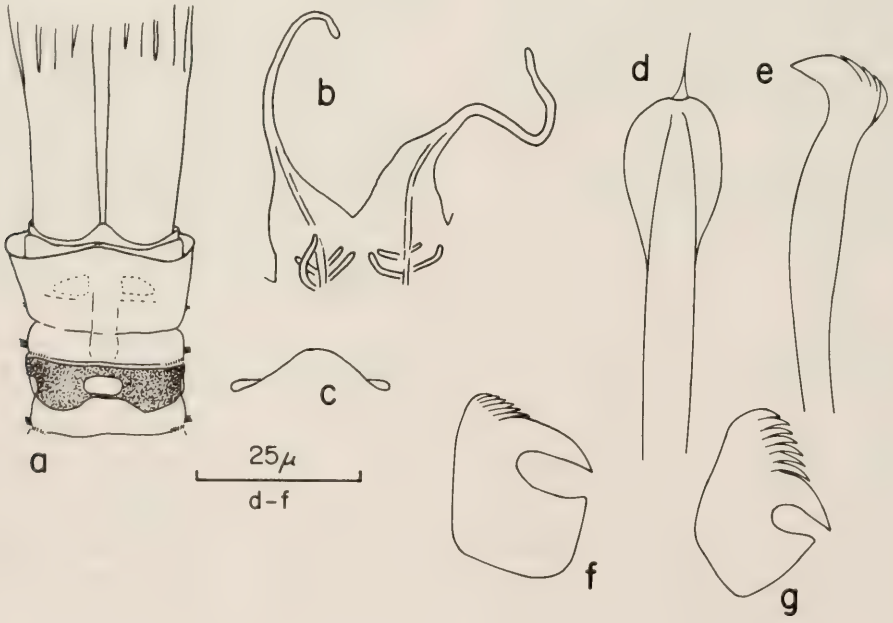

FIGURE 7.—*Chone veleronis* new species; a and c from holotype, rest from paratypes; d, f, not drawn to scale: a, ventral view of anterior end. Horizontal broken line in collar indicates anterior border of first setiger seen occasionally. The two areas on the collar encircled by broken lines remain whitish after staining with methyl green. The glandular girdle has been dotted; b, tips of two radioles; c, collar of another specimen in same view as in a; d, spatulate seta; e, thoracic uncinus; f, large uncinus from anterior abdominal setiger; g, uncinus from 40th abdominal setiger from median position in torus, 17 μ high.

abdominal setigers. The pygidium is triangular and pointed. Eggs occur from the sixth thoracic setiger.

The inconspicuous first bundle of setae originates at the level of the following notopodia. These have four to six of each upper limbate, very tiny bayonet, and pointed spatulate (Figure 7d) setae. Notopodial lips were not seen. Thoracic neuropodia contain slightly more than half a dozen long-handled uncini (Figure 7e). Abdominal setigers carry approximately half a dozen finely limbate neurosetae and, at least through the 40th setiger, 12 to 15 uncini. The uncini from the anterior abdomen, in the most recently formed sections of the tori, are of the usual form of *Chone* (Figure 7f) with several columns of five to six accessory teeth each. The smallest, i.e., oldest, uncini of these tori, and all uncini in posterior segments (Figure 7g), have smaller bases and appear similar to the uncini of *Oriopsis*. The posterior uncini have about six columns of about seven teeth each.

Staining with methyl green shows the absence of ventral shields. The whole surface in the anterior half of the body accepts the dye uniformly except for the anterior edge and ventral parts of the collar (cf. Figure 7a), the inter- and intrasegmental furrows, and the glandular girdle on the second setiger. Ventrally, the anterior border of the first setiger, which is often invisible in unstained material, is marked as a whitish line. The presetal rings of glandular tissue stain less well than the rest of the epidermis. On the posterior half of the abdomen only few epidermal cells accept the stain.

Remarks: Hartman (1959, 1965) has listed the species of *Chone*, to which *C. rosea* Hartmann-Schröder, *C. striata* Hartmann-Schröder, *C. trilobata* Gallardo, and *C. albocincta* described below should be added. Among these, *C. velero-nis* is distinguished by the ventral enlargement of the postsetal glandular girdle on the second setiger, the very long branchial bases, and the length of the palmate membrane. Only very few species (e.g., *C. arenicola* Langerhans) have a palmate membrane extending beyond the origin of the distal pinnules.

CHONE ALBOCINCTA NEW SPECIES

Figure 8

Holotype: From *Velero* station 6104, lat 33°39′45″N, long 118°06′40″W, 26 m, dark gray silty fine sand, 19 Feb. 1959. AHF Poly. 0454.

Paratypes: From same station and date. AHF Poly. 0455, three adults or near-adults, nine juveniles.

Diagnosis: A *Chone* species of intermediate size without ventral shields. Branchial basis slightly longer than the slightly oblique collar. Eight to ten pairs of radioles, connected by palmate membrane up to origins of distal pinnules, with abruptly tapered filiform free ends. Presetal whitish rings of tissue in thorax; presetal and postsetal whitish rings in anterior and median abdomen. First bundle of setae small, on same level as following notosetae. Spatulate setae with pointed tips. Anterior abdominal uncini markedly different within tori, smallest with rounded bases and high crowns. Posterior abdominal uncini predominantly of latter type.

The name of the species refers to the whitish rings contrasting in unstained animals with the red-brown color of the remaining epidermis.

Material studied: Type series.

Description: The holotype is a mature female with 8 thoracic and approximately 50 abdominal setigers. The total length is about 18 mm, the greatest width is 1 mm. The branchial crown measures about 6 mm. Two other adult animals of 51 and 52 abdominal setigers are slightly larger (total 20 mm; branchial crown, 7 mm) and somewhat shorter than the holotype. The juveniles have trunks about 5 mm long and the same body proportions. All specimens are well preserved.

The branchial crown has a base slightly longer than the collar and 9 to 10 pairs of radioles which are united by the palmate membrane up to the insertion of the distal pinnules. A 0.2-mm broad flange extends for a short distance beyond this point but tapers abruptly to a filiform free end (Figure 8a). The free ends of the radioles are

from one-fifth to one-sixth the length of the total radioles. The ends of the radioles surpass the ends of the distal pinnules. Ventral nude filaments were not seen.

The collar (Figures 8b and 8c) is oblique, with entire margin. The first (buccal) segment is invisible and the collar is not clearly set off from the first setiger; the border can be recognized only in stained material. The thoracic and 15 to 20 anterior abdominal setigers are clearly biannulate; after staining also the following ones appear divided. Ventral shields are absent. A thick glandular postsetal girdle is present on the second setiger. Dorsally in the thorax, the intrasegmental borders bend rearward similar to *C. magna* (cf. Figure 5e). Rings of elevated whitish tissue, presumably glandular, are present in the presetal annuli of the thoracic setigers and in the presetal and postsetal annuli of the anterior 15 to 20 abdominal setigers. The ring on the second thoracic setiger is ventrally expanded (Figure 8b). Except on the second se-

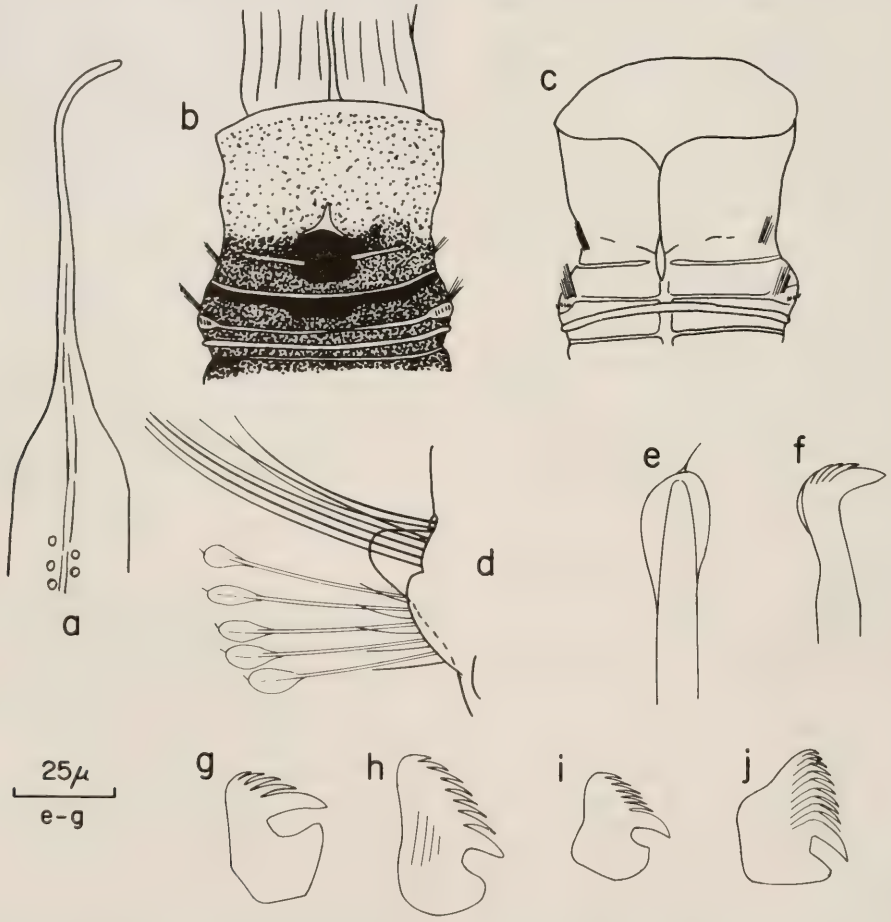

FIGURE 8.—*Chone albocincta* new species, from large types; abdominal uncini not to scale: a, end of median radiole; b, ventral view of anterior end, showing staining pattern; c, dorsal view of anterior end, branchial crown omitted; d, anterior view of fourth notopodium; e, spatulate seta; f, thoracic uncinus; g, large uncinus from fourth abdominal setiger (about 30 μ high); h, small uncinus from ninth abdominal setiger; i, j, small and large uncini from approximately 40th abdominal setiger.

tiger, the rings are invisible after using methyl green, which stains the setigers in question uniformly except for the inter- and intrasegmental furrows. Posterior to the 15th to 20th abdominal setiger, the stain is accepted by numerous, distinct cells arranged in presetal and postsetal bands. These bands coalesce in the posterior part of the abdomen.

The first bundle of setae, slightly smaller than the following ones, inserts in the collar at the same level as the following notopodia (Figure 8c). The notopodia have small lips (Figure 8d) and long limbate, bayonet-type and narrow spatulate setae; the latter have pointed tips (Figure 8e). The thoracic uncini, with small wings (Figure 8f) are arranged in single rows.

Anterior abdominal parapodia have about 30 uncini. The large (ontogenetically most recent) uncini (Figure 8g) have squarish bases and three to four rows of four or five coarse teeth. The uncini change gradually within the torus into smaller hooks (Figure 8h) with rounded bases and somewhat more teeth (five on the fourth setiger, seven on the ninth). In the posterior abdomen, the smallest uncini of a torus are similar (Figure 8i; about 10 columns of teeth); the largest ones (Figure 8j), however, have very broad posterior portions and crowns with more numerous teeth in approximately half as many rows.

Juveniles of about 5-mm trunk length and 0.4- to 0.5-mm width, with about 35 abdominal setigers, show the white rings clearly. Staining with methyl green, however, indicates that the glandularization of the epidermis is not complete. The dye-absorbing cells are distributed principally along the edges of the stained areas so that the centers of the areas are light.

Remarks: *Chone albocincta* seems to be distinguished from all other species of the genus (cf. p. 479) by the whitish segmental rings of tissue. Somewhat similar presetal rings, however, also occur in *C. veleronis* described above. Neglecting differences in size, *C. albocincta* may be separated from the northeast Pacific species without ventral shields (*C. aurantiaca, C. duneri, C. infundibuliformis, C. magna, C. mollis,* and *C. veleronis*) also by the following: the postsetal glandular girdle on the second segment is narrow ventrally (from *C. veleronis*); the first segment is indistinguishable in the first segment in unstained animals (from *C. mollis*); the radioles have long free ends (from *C. aurantiaca* and *C. infundibuliformis*); the abdominal uncini have coarse teeth (from *C. duneri*). *Chone magna* has spatulate setae without pointed tips and only one form of abdominal uncini.

EUCHONE MALMGREN, 1866 EMENDED

EUCHONE Malmgren, 1866, p. 405.- Langerhans, 1881, p. 111.- Saint-Joseph, 1894, p. 250.- Bush, 1904, p. 190.- Hofsommer, 1913, p. 327.- McIntosh, 1923, p. 281.- Fauvel, 1927, p. 339.- Berkeley and Berkeley, 1952, p. 121.- Ushakov, 1955, p. 418.- Day, 1967, p. 774.- Banse, 1970, p. 389.

Type species: *Euchone analis* (Kröyer) (cf. Bush, 1904).

Diagnosis: Sabellidae with semicircular branchial lobes sometimes united by palmate membrane. Collar conspicuous, sometimes bilobed. Postsetal girdle of glands on second setiger. Ventral shields sometimes present. Anal depression with lateral wings formed by variable number of caudal segments. Three types of thoracic notosetae: upper, or upper-anterior ones limbate; lower, anterior ones narrowly limbate (bayonet-type); and lower, posterior ones spatulate or usually subspatulate. Thoracic neuropodial uncini long-handled, acicular. Abdominal notopodial uncini avicular, with rounded or square bases; abdominal neurosetae limbate.

Remarks: The genus continues to comprise all Fabriciinae with an anal depression. Added to previous diagnoses are presence or absence of the palmate membrane, the note about the collar, the postsetal girdle of glands, the bayonet-type setae, and the ventral shields. The last three characters had previously been mentioned by Banse (1970). It must be noted that *E. alicaudata* Moore, known so far only from one specimen, possibly lacks bayonet-type setae (cf. p. 489). The number of thoracic setigers (almost

always eight) is not considered as a diagnostic character for this genus.

Of great consequence for the systematics of the Sabellidae is the opinion that the number of lobes in the collar and the presence or absence of a palmate membrane are specific characters in *Euchone*. Therefore, they cannot be used for dividing genera (cf. p. 459 and 461). The reason is my opinion that the anal depression is of monophyletic origin and therefore a primary character, sufficient to characterize *Euchone*.

EUCHONE ANALIS (KRÖYER)

Figure 9a-c

SABELLA ANALIS Kröyer, 1856, p. 17.
EUCHONE ANALIS.- Malmgren, 1866, p. 406; 1867, p. 223.- Berkeley and Berkeley, 1952, p. 121.- Pettibone, 1954, p. 339 (synonymy).- Hartmann-Schröder, 1971, p. 521.
not *EUCHONE ANALIS* Imajima, 1963, p. 367.

Diagnosis: A *Euchone* species with ventral shields, with 16 to 22 anterior abdominal setigers and 9 to 12 setigers in anal depression. Nine to 17 pairs of radioles united by palmate membrane for half their length, with free ends tapered, intermediate in length; 5 to 10 pairs of ventral nude filaments. Collar level, with slight ventral incision, almost concealing the branchial basis. Lower thoracic notosetae subspatulate. Uncini from anterior and posterior abdomen similar, with squarish bases.

Material studied: Point Barrow, northern Alaska, about 65 m. Identified by M. H. Pettibone (cf. Pettibone, 1954). USNM 23651, 1 specimen.

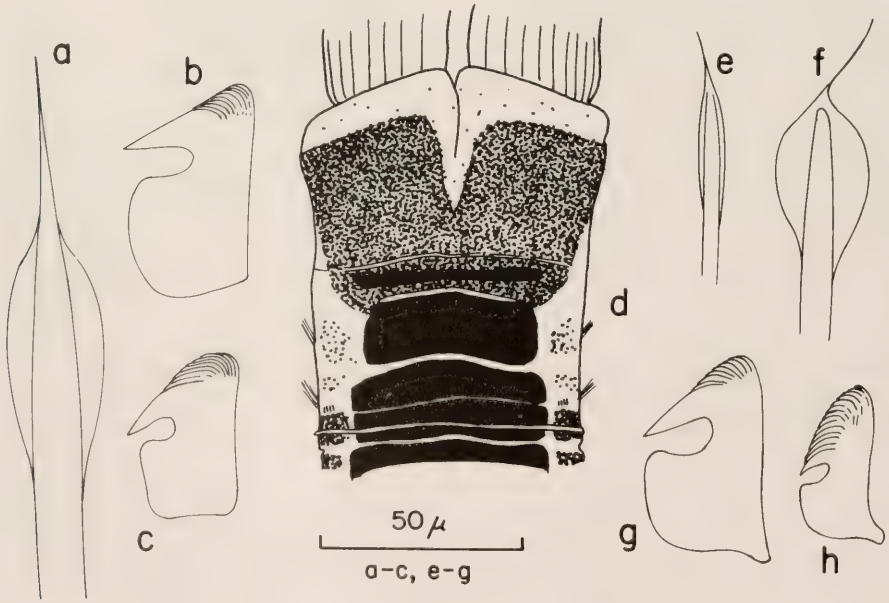

FIGURE 9.—*Euchone analis*: a, subspatulate notoseta; b, median uncinus from third abdominal setiger; c, same, from 21st. Accessory teeth schematic; *E. papillosa*: d, anterior end of thorax, ventral view, showing staining pattern; e, bayonet-type seta; f, spatulate seta; g, median uncinus from third abdominal segment; h, uncinus from anterior depression segment, approximately one and a half times enlarged over Figure g.

Addition to the Description: The specimen is complete. The length of the trunk is about 15 mm, that of the branchial crown approximately 4 mm. The branchial crown consists of some ventral nude filaments (5 to 10 pairs according to Kröyer, 1856, and Malmgren, 1866), and 10 pairs of radioles bearing pinnules and connected by a palmate membrane. The ends of the radioles are like those of *E. elegans* (cf. Figure 11a). The collar has a small ventral incision. The second setiger is ringed by a postsetal girdle of glands. Segments are biannulate up to the anal depression. There are 17 anterior abdominal segments and 9 setigers in the anal depression. Ventral shields are present in thorax and abdomen. The shields of the first segment and first setiger are divided by intrasegmental furrows which do not stand out as whitish lines after staining. In the abdomen the shields have the form depicted by Malmgren (1866, Plate 28, Figure 88).

The notopodia, including the large first one, have conspicuous lips of the same form as *E. rubrocincta* (cf. Figure 10d). The bayonet-type setae have shafts almost as thick as the subspatulate ones (Figure 9a) behind them and are terminally thin, as usual. Anterior abdominal uncini (Figure 9b) are all alike within the tori; each has a squarish basis and a crown of about 10 rows of accessory teeth in several columns. The bases of the posterior uncini (Figure 9c) are similar but the crowns have about 15 rows of teeth in approximately a dozen columns.

After staining, the ventral shields and, separate from them, areas before and behind the parapodia are conspicuous in thorax and abdomen. The first setiger does not seem to be separated from the preceding and following segments by nonstaining lines, nor is the intrasegmental furrow distinct. The intrasegmental furrow on the second setiger resembles that of *E. rubrocincta* (Figure 10c). Dorsally, the thorax and the anterior segments of the abdomen are essentially free of stain-accepting cells. In middle and posterior abdominal setigers, presetal broad rings are complete; they are visible as whitish tissue also in the unstained animal.

Remarks: This specimen has 17 anterior abdominal setigers, fewer than stated by Malmgren (1866, about 19) and Berkeley and Berkeley (1952, 20 to 22) but similar to Kröyer (1856, about 16). More material must be studied in order to see whether the number of anterior abdominal setigers overlaps those of the similar *E. elegans* and *E. rubrocincta*. If so, a probably reliable difference of *E. analis* from the others will be the form of the anterior abdominal uncini.

The record by Imajima (1963) from the west coast of Kamchatka is not this species because of the low number of anterior abdominal setigers and the high number of segments in the anal depression.

EUCHONE PAPILLOSA (SARS)

Figure 9d-h

SABELLA PAPILLOSA Sars, 1851, p. 203.

EUCHONE PAPILLOSA.- Malmgren 1866, p. 407.- Hofsommer, 1913, p. 327.- Augener, 1928, p. 805 (synonymy).- Evenkamp, 1931, p. 412.- Pettibone, 1956, p. 578 (synonymy).- Kühlmorgen-Hille, 1963, p. 51.- Hartmann-Schröder, 1971, p. 521.

SABELLA TUBERCULOSA Kröyer, 1856, p. 18.

EUCHONE TUBERCULOSA.- Malmgren, 1866, p. 407.

Diagnosis: A large *Euchone* species with ventral shields, with at least 21 abdominal setigers; 8 to 10 form anal depression. Ten to 15 pairs of radioles connected for approximately one-half their length by palmate membrane, with long filiform free ends. Two to five pairs of ventral nude filaments. Collar oblique, with midventral incision, scarcely concealing the branchial basis. Very conspicuous round fields of glands ventrally in abdomen. Spatulate setae with very long tips. Uncini of anterior abdomen with small crowns of teeth and bases with posterior extension; markedly higher crowns in posterior abdomen.

Material studied: Kiel Bight, western Baltic (unknown locality). Collected and identified by G. Kühlmorgen-Hille (cf. Kühlmorgen-Hille, 1963). Part of sample, USNM 45390, 6 specimens.

Additions to description: Because the species is well known, only some characters have been studied, mostly for a comparison with *E. capensis* Day and *E. velifera* new species, both of which also have collars with ventral incisions. The animals studied were fixed in their tubes, are up to 2.5 cm long, and are well preserved.

The radioles have free filiform ends as shown by Malmgren (1866, Plate 29, Figure 92G but not 94G). The collar (Figure 9d) is markedly longer ventrally than dorsally. The number of abdominal segments in six animals is 21, 21, 22, 23, 23, and 24, of which 8 to 10 form the anal depression. Similarly Hofsommer (1913) found specimens from the western Baltic, which he believed to be juveniles, with a total of 29 segments (= setigers, from the context) and stated that in adults the number is constantly 35, similar to Malmgren (1866). Evenkamp (1931) in material from Kiel Fjord, however, observed up to 62 segments of which, again, 8 were thoracic.

Thoracic notopodia contain broad bayonet-type setae (Figure 9e) and spatulate setae (Figure 9f). The spatulate setae in the present material are broader than those depicted by Malmgren (1866, Plat 29, Figures 92B[1] and 94B[1]). The uncini on anterior abdominal segments (Figure 9g) have broad bases with small posterior appendages and crowns with approximately 10 columns with 10 to 13 teeth each, depending on the size of the uncini. Posteriorly in the abdomen, the bases of the uncini become more rounded, and there are about 15 rows of teeth in much enlarged crowns (Figure 9h).

The thoracic and abdominal ventral shields are very conspicuous even in unstained material (cf. Malmgren, 1866, Plate 29, Figures 92 and 94). After using methyl green, the ventral pattern in the anterior thorax is as shown in Figure 9d. Laterally in the thorax, crescentic areas of stained tissue occur posterior to the parapodia and to a lesser degree anterior to them. The dorsal side of the thorax is unstained except for a pair of conspicuous rounded areas near the anterior border of each segment from the 4th setiger onwards. In the anterior and middle regions of the abdomen, each setiger shows ventrally two pairs of rounded patches, one near the anterior and one near the posterior border. These have been figured first by Malmgren (1866, Plate 29, Figures 92 and 94). Their size varies among individuals; they sometimes occupy almost half of the ventral area of the segments. Laterally in the abdomen, the stained tissue around the parapodia, observed in the thorax, becomes gradually larger and extends onto the dorsal side so that from the middle of the abdomen, a pigmented band crosses the posterior part of the segments (the parapodia insert here posteriorly on the segments). In the same region, the anterior dorsal patches coalesce. Shortly before the depression segments, the intrasegmental furrows disappear and each segment is uniformly stained both dorsally and ventrally.

EUCHONE RUBROCINCTA (SARS)

Figure 10

CHONE RUBROCINCTA Sars, 1862, p. 128.
EUCHONE RUBROCINCTA.- Malmgren, 1866, p. 406.- Southern, 1914, p. 144.- McIntosh, 1916, p. 33; 1923, p. 282.- Southward, 1956, p. 278.

Diagnosis: A *Euchone* species with conspicuous ventral shields, with 11 to 15 anterior abdominal setigers and up to 12 setigers in anal depression. Up to 16 pairs of radioles united by palmate membrane for about half their length, with long free ends. Up to eight pairs of nude filaments. Collar level, with a small ventral notch. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with small crowns of teeth, slim necks, and narrow bases with marked posterior extensions. Uncini of posterior abdomen with large crowns, without necks.

Material studied: Syntypes, from Florø, near Bergen, Norway, approximately lat 61°40′N, long 5°00′E, stony bottom (Sars, 1862). ZMO, 3 specimens.

Ballynakill Harbour, Northwest Ireland, stations L 245, L 310, and ML L 11a (cf. Southern,

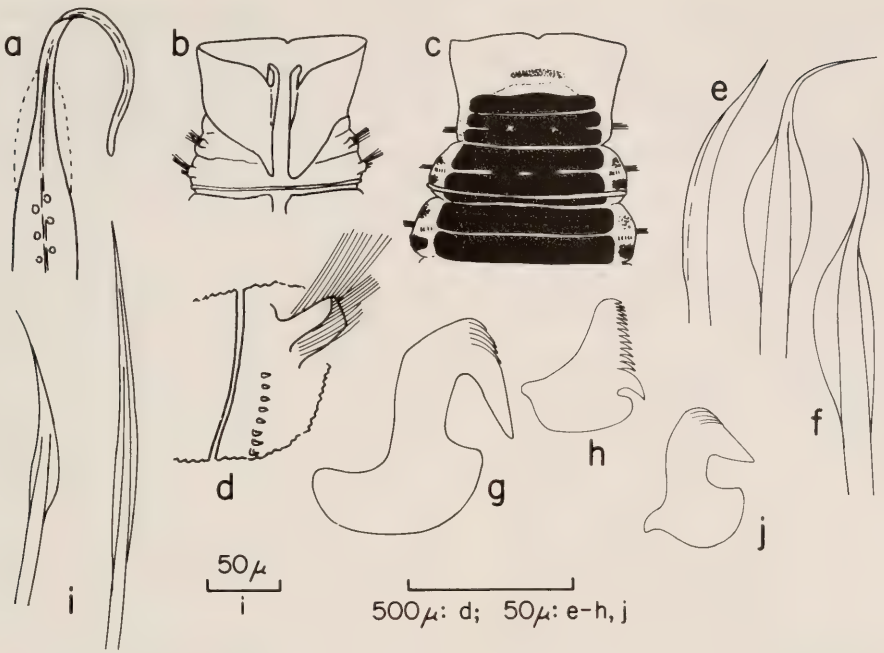

FIGURE 10.—*Euchone rubrocincta*; b-h from syntypes, a and i from NMI, j from Southward's material: a, end of representative radiole. Broken line indicates extent of flange in syntypes (see also text); b, dorsal view of anterior end, branchial crown omitted; c, ventral view of anterior end, branchial crown omitted, after staining. Slightly schematic; x indicates the extent of the incision of the ventral shield on the first setiger of *E. elegans*; d, part of lateral body wall of second setiger, seen slightly from below and behind, with setae and glandular girdle; e, f, bayonet-type and two subspatulate setae from fifth thoracic setiger; g, anterior abdominal uncini (seventh abdominal setiger). Accessory teeth schematic; h, uncinus from depression segment (17th abdominal setiger); i, subspatulate and limbate setae from sixth thoracic setiger; j, uncinus from seventh abdominal setiger.

1914). NMI 77.1908, 1 specimen from each station.

Irish Sea, station 22 of Southward (1956, 1957). Dr. E. C. Southward's private collection. 3 specimens.

Additions to the Description: The largest of the well-preserved syntypes, a fairly relaxed specimen, is approximately 2.5 cm long of which about one-fourth is contributed by the branchial crown. The width is about 2 mm. The other syntypes are approximately two-thirds as long; in one of them, a mature female, the branchial crown contributes about one-third of the total length, in the other one it is lost.

The branchial crowns of the two complete specimens consist of 10 and 13 pairs of radioles with pinnules and up to 8 pairs of slender naked ventral filaments. Two to three pairs of the latter are very short, and one or two pairs are as long as the radioles. The radioles are united for about half their length by a conspicuous palmate membrane. They end in bare tips, proximally broad owing to the continuation of the palmate membrane, but narrow in the terminal sections. The latter tend to be shorter ventrally than dorsally and are, on the average, about half as long in the syntypes as in the material from northwestern Ireland (Figure 10a). The length of the sections of the radioles free of pinnules is very approximately one-eighth of

the total length in the syntypes and in Southern's material.

In the syntypes, the collar is of equal height dorsally and ventrally and has only a small ventral notch (Figures 10b and c). Setigers are biannulate, which is especially obvious in the thorax. In the three syntypes, there are 11 anterior abdominal, 1 transitional, and 11 depression setigers; 15, 1, 9; and 12, 0, 10 setigers, respectively. Ventral shields are distinct in the thorax and abdomen as depicted by Malmgren (1866, Plate 29, Figure 91).

The thoracic notopodia (Figure 10d) are very conspicuous; each contains about a dozen each of long limbate, short bayonet-type (Figure 10e), and subspatulate (Figure 10f) setae. The long limbate setae originate above the semicircular lip shown in Figure 10d which is about 0.2 mm long; the other two kinds below it. Each neuropodium contains approximately 1½ doz of long-handled hooks of the usual form (cf. McIntosh, 1923, Plate 131, Figure 2a). The uncini of the anterior abdomen (Figure 10g; cf. Figure 10j) do not have the squarish basis usually found in *Euchone* species but have a slim neck and a large posterior extension making them almost S-shaped. Even the dorsalmost ones in the tori studied have essentially this outline. Only a few columns of teeth are found in these uncini. The uncini of the depression segments are formed as shown in Figure 10h; they have approximately eight columns of teeth, and the number of rows is 12 to 14. The number of uncini is about 2 doz per torus anteriorly in the abdomen and in median segments of the anal depression. The abdominal capillary setae are arranged in two series per neuropodium.

After using methyl green, the collar (Figure 10c) is lightly stained except for a ventral unstained area and, in some animals, a diffuse band anterior to it. The thoracic ventral shields are clearly marked. Laterally strongly staining areas are found posterior to and, to a lesser degree, anterior to the thoracic parapodia. In the last thoracic segments, these areas touch the ventral shields but do not continue onto the dorsal side, except as traces. In the abdomen, however, the stained cells form two girdles around each segment, interrupted only by the fecal groove; the presetal ring, which may appear dorsally as whitish glandular tissue even in unstained material, stains more strongly than the postsetal one. The ventral shields are not markedly darker after staining than the lateral and dorsal parts. The intersegmental unstained furrows disappear gradually in the depression segments.

In the material from northwestern Ireland, the largest animal, a mature male, is almost 2.5 cm long, of which about one-third is contributed by the branchial crown; the smallest specimen is 1.5 cm long. The latter has 11, the former, 15 pairs of radioles, with about 4 doz pairs of pinnules each. In all specimens, there are 12 anterior abdominal setigers, the twelfth sometimes appearing to be a transitional segment, and 10 to 12 depression segments. The notopodia (cf. Figure 10d) appear to be divided into anterior and posterior lips, rather than form one semicircular fold. Limbate and subspatulate notosetae are shown in Figure 10i; the total number of notopodial setae is 2 doz. The other characters agree with the syntypes.

No color is left in the syntypes of the Irish material, but Southern (1914) stated that the bright red bands, which gave the species its name, were present in Formalin-preserved material until the transfer into alcohol. Sars (1862) observed one purple ring on each segment.

McIntosh (1916) reported on animals with 15 to 16 pairs of radioles. It must be noted that McIntosh's description (1916, also 1923) of other features of the branchial crown contains quotations of Southern's (1914) text for *E. rosea*.

Southward's specimens are small, up to 7 mm long. Two have 11 anterior abdominal setigers, and one transitional setiger; the third animal has 13 or 14 anterior abdominal setigers. An uncinus from this region (Figure 10j) has a broader neck than the material treated above but otherwise has the same characteristic form. The staining pattern is as described by the syntypes as far as this can be recognized in the previously dried specimens.

Remarks: *Euchone rubrocincta* is close to the smaller *E. elegans* Verrill from which it is

distinguished by the larger number of radioles with long slender ends, and especially the form of the anterior abdominal uncini. Further, the incision of the ventral shield at the level of the first parapodium is very short in *E. rubrocincta* (see also *E. analis*, p. 483). *E. rosea* Langerhans, as described by Banse (1970) for specimens from the Ivory Coast, is very similar in regard to the tips of the radioles, the collar, the subspatulate notosetae, and especially the abdominal uncini. However, the ventral shield on the first setiger is not divided, and the number of anterior abdominal setigers is only 10 or 11, and that of the anal depression only 6. The smaller number of radioles in the African material may be due to their smaller size.

The distribution of the species is not well known. Material of Southern (1914) and Southward (1956) collected around Ireland has been treated above. The specimens of Malmgren (1866) from the Skagerak and McIntosh (1916, 1923) from the Shetlands are certainly *E. rubrocincta*. The species is also reported from the Mediterranean Sea (cf. Fauvel, 1927), but I have not searched the literature for Lusitanian and more southern records. Also, the reports of *E. rubrocincta* from the northwest Atlantic by Moore (1909) and Baillie (1946) should be checked because of the possible confusion with *E. elegans* treated below. The former author did not give any reference for identification; the latter referred to Malmgren's description.

EUCHONE ELEGANS VERRILL

Figure 11a-e

EUCHONE ELEGANS Verrill, 1873, p. 618.-Hartman, 1944a, p. 334 (with other references).

Diagnosis: A *Euchone* species with ventral shields, with 12 to 15 anterior abdominal setigers and 8 to 10 setigers in anal depression. Six to eight pairs of radioles, united by palmate membrane for about half their length, and rather broad and free ends. Three to four pairs of nude filaments. Collar level, with small ventral notch. Lower thoracic notosetae subspatulate. Marked divergence of uncini within tori of anterior abdomen; ontogenetically recent uncini with broad bases and small posterior extension; old uncini with rounded bases and high crowns, similar to those in depression.

Material studied: Syntypes, collected from Block Island Sound, Mass., in 1871. USNM 7513, 5 specimens.

Cape Cod Bay, Mass., SEP station 1412 E5, lat 41°55.0'N, long 70°08.5'W, 33 m, muddy sand, 11 June 1968. SEP, 4 specimens. Unpublished record.

Cape Cod Bay, Mass., SEP station 2318 Ep, lat 41°45.0'N, long 70°06.5'W, 16 m, sand, 13 Oct. 1966. SEP, 22 specimens. Unpublished record.

Additions to the Description: The available specimens are up to 1 cm long; about one-third of the length is contributed by the branchial crown. Verrill (1873) observed animals up to 2 cm long. Most of the branchial crowns have seven pairs of radioles with up to 3 doz pinnules each and three to four pairs of ventral nude filaments; one pair of these is about as long as the radioles. The free ends (Figure 11a) contribute about one-sixth of the total length of the radioles. The collar is of equal height dorsally and ventrally and has only a small ventral notch. Segments are biannulate, particularly in the thorax. A postsetal girdle of glands is present on the second setiger. Ventral shields are moderately visible in unstained material in the thorax and anterior abdomen but stand out clearly upon staining. In the syntypes, the number of abdominal setigers is 13 (12 in one) followed by 1 transitional and 8 depression setigers. In the 10 SEP specimens, up to 9 mm long, 15 setigers are present prior to the beginning of the depression in 7 specimens; 14 setigers in 2 specimens; and 14 or 15 in 1 specimen. The anal depression extends through 10 setigers in the largest animals.

The thoracic notopodia are almost as conspicuous as in *E. rubrocincta* (cf. Figure 10d). Each contains long limbate, short bayonet-type, and subspatulate (Figure 11b) setae, totaling less than a dozen. Each neuropodium has about 10 long-handled hooks. The uncini of the anterior abdominal segments (Figure 11c) have a broad

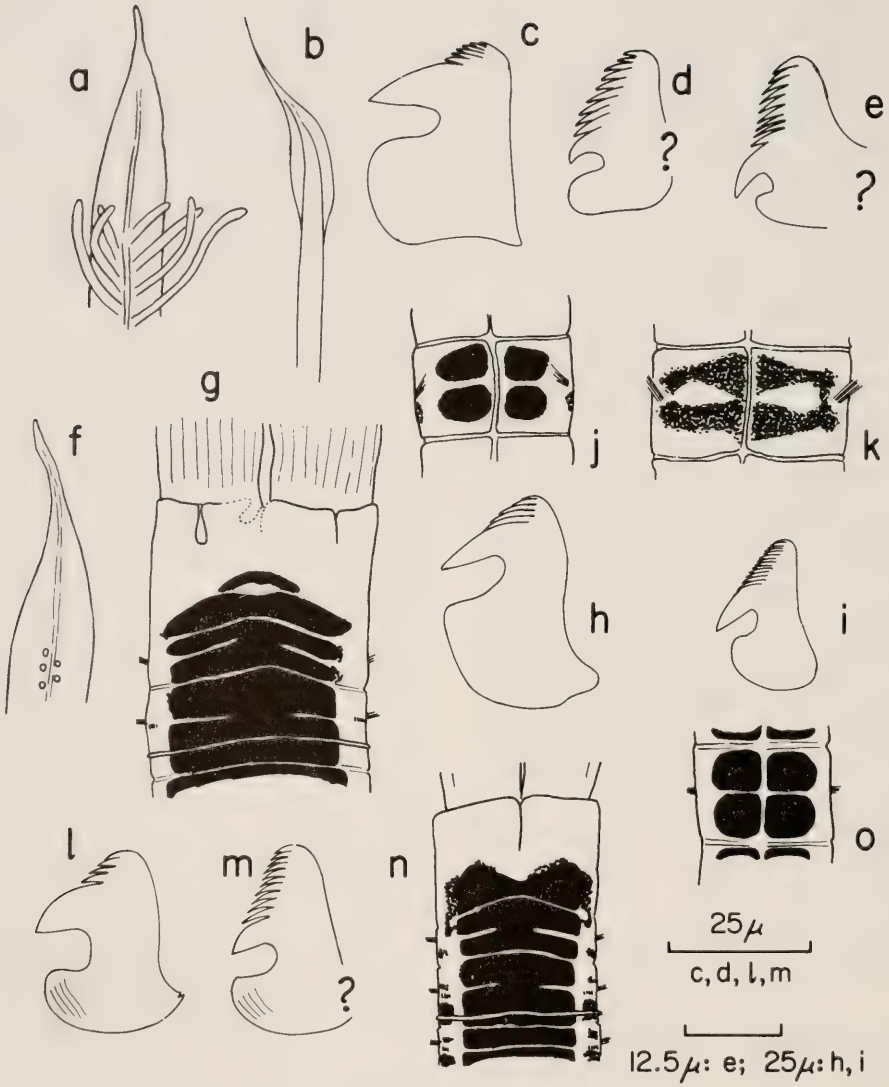

FIGURE 11.—*Euchone elegans*; a, c, d from syntypes, b, e from SEP stn. 2318Ep; a, end of medio-ventral radiole; b, subspatulate notoseta; c, d, middle and dorsalmost uncini from second abdominal setiger; e, uncinus from 17th abdominal setiger (depression); *E. alicaudata*, from holotype: f, end of median radiole; g, ventral view of anterior end of thorax after staining; h, i, uncini from second and 18th abdominal setigers; j, ventral view of middle abdominal segment after staining; k, dorsal view of middle thoracic segment; g, j, and k are oriented in the same way; *E. capensis*, from paratypes: l, m, uncini from second and 19th abdominal setigers, the latter slightly enlarged; n, o, ventral views of anterior end of thorax and median abdominal segment after staining, slightly schematic.

square base similar to those of many other *Chone* and *Euchone* species. The dorsalmost and ontogenetically oldest ones (Figure 11d), have a much higher crown with about 10 rows of teeth and are similar to the uncini in the depression segments (Figure 11e).

After staining with methyl green, the pattern on the first setiger agrees with that of *E. rubrocincta* (cf. Figure 10c) where the incomplete division of the ventral shield reaches somewhat closer to the midline than that of the second one (Figure 10c, marked by x).

Remarks: *Euchone elegans* is close to *E. rubrocincta* from which it is distinguished by the much smaller number of radioles and their short free ends and the form of the uncini of the anterior abdominal segments. The division of the ventral shield at the level of the first parapodium is marked. The species is also similar to *E. analis* as described by Malmgren (1866, 1867; cf. p. 482) but has slightly fewer anterior abdominal setigers. The posterior abdominal uncini of *E. analis* are similar to the anterior ones but are markedly different in *E. elegans*.

EUCHONE ALICAUDATA MOORE AND BUSH

Figure 11f-k

EUCHONE ALICAUDATA Moore and Bush, 1904, p. 165.

Diagnosis: A large *Euchone* species with ventral shields, with 22 abdominal setigers; 8 form anal depression with broad wings. Fifteen to 20 pairs of radioles connected by palmate membrane for one-quarter of their length, with broad flanges extending beyond distal pinnules, and tapering to slender tips. Several pairs of ventral nude filaments. Collar level, with ventro-lateral incisions or folds, probably ventrally incised, concealing the branchial basis. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with strong necks and bases with posterior extensions; uncini of the posterior abdomen with high crowns.

Material studied: Holotype from 280 m near Tokyo. USNM 5496.

Additions to the Description: The radioles number somewhat more than 15 as stated in the original description; they end in tips as shown in Figure 11f. The collar (Figure 11g) appears to have ventro-lateral incisions rather than folds, as originally stated; owing to injury the presence or absence of a marked midventral incision, implied by Moore and Bush (1904), cannot be verified. A postsetal girdle of glands is present on the second setiger. Bayonet-type setae were not found on the two dissected thoracic notopodia. In this respect, *E. alicaudata* is unique among the 25 species of *Chone* and *Euchone* I have studied; an investigation of more specimens is very desirable. The subspatulate setae were correctly depicted by Moore and Bush (1904, Plate 11, Figure 15). The uncini of the anterior abdomen (Figure 11h) have a posterior extension which is not so distinct in depression segments (Figure 11i). The latter, however, have high crowns with 13 to 15 rows of teeth.

The ventral shields are distinct in thorax and abdomen, becoming even more marked after staining (Figures 11g and 11j). The shields of the first and second setigers are not completely divided by the intrasegmental furrows. The dorsal thoracic staining pattern is shown in Figure 11k. In the abdomen, simple broad bands extend from the level of the parapodia across the dorsum except in the segments of the anal depression where the intrasegmental furrows disappear.

Remark: *Euchone capensis* Day bears some resemblance to *E. alicaudata*, but the species are well distinguished by the form of the ventral shields on the first (buccal) segment (cf. Figures 11g and 11n).

EUCHONE CAPENSIS DAY

Figure 11l-o

EUCHONE CAPENSIS Day, 1961, p. 540; 1967, p. 776.

Diagnosis: A *Euchone* species with ventral shields, with 25 to 32 abdominal setigers; 7 or 8 form anal depression. Nine pairs of radioles,

united by palmate membrane for two-thirds of length, with very long filiform tips. Two to three pairs of ventral nude filaments. Collar approximately as long as branchial basis, with deep ventral incision. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with strong necks and few rows of teeth, bases with small posterior elongation; uncini of posterior abdomen with greatly enlarged crowns.

Material studied: Paratypes from Stn. TRA. 73M, off South Africa, Ecological Survey, UCT. 311 m. Material at UCT, 3 specimens.

Additions to the Description: The radioles are flanged some distance beyond the palmate membrane. Many pinnules of the middle sections of the radioles extend as far as the end of the distal pinnules. The very long and filiform tips of the radioles extend beyond this level. Whereas Day (1961, Figure 14t; 1967, Figure 37.6j) depicted the branchial base as not concealed by the collar; the branchial base in at least one of the paratypes is hidden. A postsetal girdle of glands is present on the second thoracic setiger. The ventral shields are divided within each thoracic segment. While Day (1961) reported 32 abdominal setigers for the holotype, 2 complete specimens have 25 and 25 or 26 abdominal setigers; 7 or 8 form the anal depression.

An uncinus from the anterior abdominal region is shown in Figure 11l (cf. Day, 1961, Figure 14n). The uncini of the posterior region seem to be similar except that the number of rows of teeth above the main fang is about 10 (Figure 11m). The number of uncini is anteriorly just below, posteriorly slightly above, a dozen per torus.

After using methyl green, the ventral shields are bordered laterally by unstained epidermis (Figure 11n), except in the first thoracic setigers. In the abdomen, intra- and intersegmental borders appear broader than in the thorax, and the outline of the shields becomes rounded (Figure 11q); they are almost circular large patches anterior to the anal depression. Broad, lateral areas of staining cells are present on the first and second thoracic setiger, and a small anterior and a large posterior patch are found around each parapodium on the subsequent segments. These patches seem to be characteristic for the species. The posterior patches tend to form crescents around the parapodia in the abdominal segments. From about the middle part of the abdomen, bands of scattered staining cells cross the dorsal side forming two bands per setiger and becoming most distinct on the depression segments.

Remarks: *Euchone capensis* has abdominal uncini that are somewhat similar to those of *E. alicaudata*, *E. rosea*, and *E. rubrocincta*. The ventral incision in the collar and the distinct abdominal ventral shields separate the South African form clearly from the two latter species. A clear distinction between *E. capensis* and *E. alicaudata* is provided by the form of the ventral shields of the first (buccal) segment (cf. Figures 11g and 11n).

EUCHONE VELIFERA NEW SPECIES

Figure 12

EUCHONE sp. Hartman, 1955, p. 114.

Holotype: Off Catalina Island, Calif., *Velero* station 2412, lat 33°30′02″N, long 118°12′02″W, 593 m, fine mud, 17 Sept. 1953 (cf. Hartman, 1955). AHF, Poly. 0256.

Paratypes: Off Point Vincente Light, Calif., *Velero* station 4854, long 33°47′30″W, lat 118°30′00″W, 179 m, 8 Feb. 1957. AHF Poly. 0453, 2 specimens.

Diagnosis: A large Euchone species with indistinct ventral shields, with 27 to 32 abdominal setigers; 7 to 9 form anal depression with large wings. Nine to 10 pairs of radioles united by palmate membrane for half of their length at least in juveniles, with short filiform free ends. Collar with lateral notches, ventrally deeply incised and folded in between the two halves of the branchial crown, concealing branchial basis. Lower thoracic notosetae subspatulate. Uncini of anterior abdomen with small crowns and square bases; uncini of posterior abdomen with

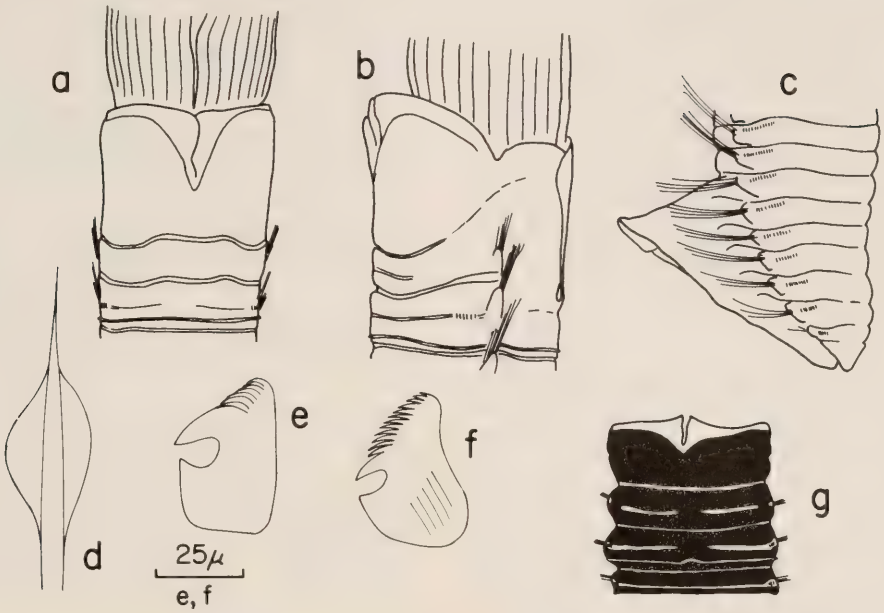

FIGURE 12.—*Euchone velifera* new species; c-e from holotype, a, b from paratypes; a-c, g not drawn to scale: a, b, ventral and left side views of anterior end of juvenile specimen; c, posterior end from the left side; d, subspatulate thoracic seta; e, f, uncini from fifth and 27th (sixth to last) abdominal segments. Accessory teeth schematic; g, anterior end in ventral view showing staining pattern.

high crowns and rounded, posteriorly enlarged bases.

The name refers to the sail-like wings of the anal depression.

Material studied: Type series.

Description: The holotype is a complete, well-preserved mature female of almost 3-cm total length (trunk length 17 mm) and 1.5-mm width. The paratypes are juveniles. In the holotype the branchial crown contributes a little more than one-third of the total length. The 9 or 10 pairs of pinnulated slender radioles are in the holotype free from each other through their entire length and have only rudimentary flanges. The juveniles have a palmate membrane uniting the radioles for approximately half of their length. The pinnules, which are of a uniform, relatively short length, are present almost to the ends of the radioles so that there are only relatively short filiform free tips. A few thin naked filaments are also present, the longest one being about half as long as the radioles. Triangular lips occur on both sides of the mouth.

The collar (Figures 12a and 12b) is slightly longer ventrally than dorsally. The dorsal gap is narrow; laterally there is a small notch. Ventrally, a deep incision is formed by the collar being folded inward between the two halves of the branchial crown. A postsetal girdle of glands encircles the second setiger. The ventral shields of unstained specimens are more distinct in the juveniles than in the adult animal. They are indicated more by the appearance of the ventral and lateral epidermis in the thorax, as contrasted to that of the dorsal side, than by morphological elevation (pads) on the ventrum. This is borne out by staining. In the adult, very conspicuous, subepidermal tissue of a creamy color is present dorsally from the third setiger, having the

appearance of ventral shields. The intrasegmental division of this tissue into anterior and posterior sections is particularly obvious in the abdomen. In contrast to shields, this material is not stained by methyl green. The very large wings of the anal depression are shown in Figure 12c.

Each thoracic notopodium after the first setiger contains three series of setae: about a dozen limbate, about half a dozen bayonet-type setae with very small wings, and 2 doz subspatulate setae (Figure 12d). The thoracic hooks are of the ordinary kind. An uncinus from the anterior abdominal region is shown in Figure 12e; there are about 8 teeth above the main fang in the smaller, and about 10 teeth in the larger, hooks of a torus. Uncini from the posterior regions differ markedly (Figure 12f), not only because of an increase of the number of teeth above the main fang but also by a marked posterior enlargement. There are about half a dozen ventral limbate setae in each abdominal neuropodium with very narrow wings.

The color of the preserved holotype is pale red-brown, except for the dorsal creamy tissue. Very numerous polygonal eggs have diameters up to 150 μ. The tube is clearly constructed by the successive addition of rings of mucus and mud.

After using methyl green, the collar is dorsally fully stained except at the anterior margin; the ventral pattern is indicated in Figure 12g; the patterns on the fourth and following setigers are the same as those on the third. In the abdomen, the intrasegmental divisions appear broader in the thorax so that, owing to the fecal groove, four rectangular fields of pigment per segment are seen. Laterally in the thorax and abdomen, the stained epidermis extends from the shields around the parapodia, uniting immediately dorsal to the notopodia. Staining cells are absent dorsally in the thorax but appear as faint lines in the abdomen.

The two young specimens (paratypes) are about 10 mm long and 0.5 to 0.6 mm wide. The approximately six pairs of radioles are almost as long as the trunk and united by the palmate membrane for about half their length. The collar (Figure 12b) is not as level as in the holotype. The number of abdominal setigers is difficult to ascertain but seems to be 27 or 28 in one, with 7 setigers in the anal depression, and 29 in the other specimen, with 9 setigers in the anal depression.

The smallest uncini in the third and fourth abdominal setiger of one of the specimens were very similar to Figure 12f, that of an uncinus of the adult animal from the posterior segments. The staining pattern is similar to that of the holotype except for a lateral tongue of nonstaining tissue which extends latero-ventrally between the posterior border of the collar, at the level of the lateral notch, and the first parapodium.

Remarks: *Euchone velifera* is unique in regard to its very deeply bilobed collar. Distinct midventral incisions are also known for *E. papillosa* and *E. capensis*. The latter two species lack laterally notched collars and very large wings in the anal depression.

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A MODEL FOR OPTIMAL SALMON MANAGEMENT[1]

Douglas E. Booth[2]

ABSTRACT

Considerable attention has been given in the literature recently to continuous time dynamic maximizing models for fisheries in general, but the time discreteness and interdependency problems encountered in the case of most salmon fisheries have been largely ignored. Hence, a discrete time profit maximizing model for a salmon fishery is developed in this paper, and it is shown that a correct salmon management policy takes the form of an investment decision with respect to the level of escapement and that a management policy of maximum sustained yield may be incorrect from an economic standpoint. It is hoped that continued research including construction of a working model will provide some indication of the difference between the magnitude of spawner stocks selected on the basis of maximum sustained yield and stocks selected on the basis of economic optimality.

Continuous time dynamic maximizing models have been developed in the literature recently to handle the problem of optimally managing a fishery resource (Brown, 1969[3]; Quirk and Smith, 1970[4]). The continuous time approach to analyzing management policy for a salmon fishery tends to be unrealistic since the reproductive process for salmon is periodic, and for certain species reproduction involves rather complex time interdependencies. In the simplest case salmon spawned in a given time period will return to their spawning ground in some future time period, while in more complex cases salmon spawned in a given time period will return to their spawning grounds in several different runs over a number of time periods; also, the level of spawning activity in one time period may affect the fertility of the spawning grounds in future time periods. Such discreteness and time interdependencies cannot be adequately characterized in a continuous time mathematical model.

Hence, the purpose of this paper is to develop a discrete time maximizing model based on currently accepted views of biological spawner-return relationships for salmon; the model is developed with the biological properties of the Bristol Bay fishery foremost in mind (Mathews, 1967). It is shown that a correct fishery management policy takes the form of an investment decision with respect to the level of escapement and that a management policy of maximum sustained yield may be incorrect from an economic standpoint. In essence the fishery manager must decide whether to invest in spawners which yield a return of additional fish at future points in time, or to catch and sell potential spawners today.

In the first section of the paper, the notation and assumptions of the analysis are presented, and in the second section, a simple first-order difference equation model of a salmon fishery is developed and discussed. In the third section, the model is extended to account for the fact that salmon spawned in time period t will return to the spawning grounds in time periods $t+4$, $t+5$, and $t+6$, and also to account for the possibility that fish spawned in time period t will deplete the spawning grounds of food to such an extent that the number of fish the spawning grounds can support in time period $t+1$ will be reduced. Desirable refinements and applications of the model

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[3] Brown, G. W., Jr., 1969. An optimal program for managing common property resource with congestion externalities. Univ. Washington, Seattle. [Mimeograph.]

[4] For a static linear-programming model useful for analyzing fishery management problems see Rothschild and Balsiger, 1971.

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are discussed in the concluding section. In the Appendix the continuous time analog to the simple model is presented.

NOTATION AND ASSUMPTIONS

The notation to be used is as follows:

R_t = the size of a run of salmon into a given river in time period t;
S_t = the number of spawners allowed to escape up the river in time period t;
x_t = the catch of salmon from a given river in time period t;
E_t = the amount of effort used to catch x_t salmon in time period t;
P_E = the price per unit of effort;
P_x = the price per unit of fish;
r = the appropriate discount rate;
T = the total number of years.

The assumptions of the analysis are as follows:

(i) The industry catch for a given river, x_t, is a linear homogeneous function of the amount of effort employed E_t and the size of the run R_t:

$$\begin{aligned} x_t &= F(E_t, R_t) \\ &= R_t\, F(E_t/R_t, 1) \\ &= R_t\, f(k_t); \text{ where } k_t = E_t/R_t.^5 \end{aligned}$$

(ii) The biological spawner-return relationship is of the form developed by Ricker (Mathews, 1967):

$$R_t = a\, S_{t-1}\, e^{(-bS_{t-1})}.$$

A graph of this function for a simple first order model appears in Figure 1. If a policy of maximum sustained yield is followed, the escapement in year t—1, S^0_{t-1}, occurs where $R_t - S_{t-1}$ is a maximum, or where

$$\frac{d\ (S_{t-1}\ a\ e^{(-bS_{t-1})} - S_{t-1})}{d\ S_{t-1}} =$$

$$a\ e^{(-bS_{t-1})}(1 - b\ S_{t-1}) - 1 = 0.$$

The escapement in year t is:

$$S_t = R_t - R_t\, f\ (k_t).$$

(iii) The appropriate objective function to maximize is assumed to be

$$\sum_{t=0}^{T-1} \frac{1}{(1+r)^t}\left[R_t\, f(k_t)\ P_x - R_t k_t P_E \right] + \frac{1}{(1+r)^T}\, G(R_T)$$

where the expression on the left is the present worth of industry profits over T—1 years, and the second expression is the present worth of a value function for the terminal stock of fish.

(iv) The price of fish P_x and the price of effort P_E are assumed to remain constant for all time periods.

For some readers the purpose of making these assumptions may at this point appear unclear. Hopefully, the comments to follow will clarify any ambiguities.

In assumption (i) a linear homogeneous aggregate production function is selected for its convenient mathematical properties, and because it has an important economic property, constant returns to scale. In most industry aggregate production function studies, the assumption of constant returns has been found to be reasonably realistic. However, in the case of the salmon industry, this hypothesis has yet to be tested.

The spawner-return relationship specified in assumption (ii) has the usual properties of fishery recruitment functions. It is clear from the graph that spawner stocks to the right of the point $\bar{S}_{t-1}$, where R_t is a maximum as a function of S_{t-1}, are irrelevant from a policy standpoint, since for any feasible run size R_t there corresponds a spawner stock S_{t-1} with $S_{t-1} \leqslant \bar{S}_{t-1}$. Note that no species interaction is implicitly assumed.

The assumption that the present worth of industry profits is the appropriate objective function to maximize is an assumption commonly made in economic analysis. Other types of ob-

[5] The first derivative of f will be denoted f'.

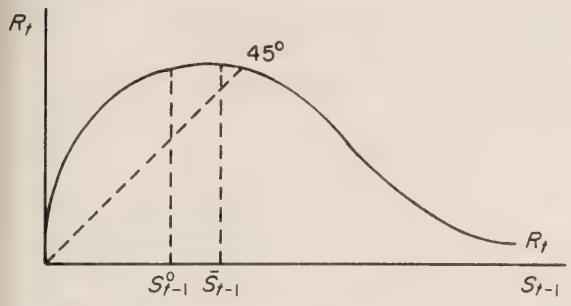

FIGURE 1.—The Ricker spawner-return relationship for salmon.

jective functions are mathematically feasible, but it is not obvious what they might be without going beyond the scope of this paper and undertaking a political analysis of salmon fishery management. Specifying a terminal value function is a mathematical necessity and will be discussed later.

Assumption (iv) implies, among other things, that the catch x_t from the salmon stock being analyzed is not large enough to influence the total industry price structure for salmon and that the factor supply market for effort, E_t, is competitive.

The problem of gear congestion on the fishing ground is adequately dealt with elsewhere and is avoided here by assuming that the fishery management authority undertakes appropriate policies to insure that only efficient levels of effort are employed (see footnote 3; Quirk and Smith, 1970). It is also assumed that salmon are not caught on the high seas but are harvested as they return to the river to spawn.

A SIMPLE MODEL

In this section the simplest type of spawner-return relationship is examined where salmon spawned in time period t—1 return to their spawning ground in time period t. Given the assumptions of the above section, the problem is to maximize

$$\sum_{0}^{T-1} \frac{1}{(1+r)^t}\left(R_t f(k_t) P_x - R_t k_t P_E\right) + \frac{1}{(1+r)^T} G(R_T),$$

subject to:

$$S_t = R_t - R_t f(k_t), S_t \geqslant 0, k_t \geqslant 0, R(0) = R_0,$$

and

$$R_t = a S_{t-1} e^{(-bS_{t-1})}.$$

The appropriate Lagrangian for the maximization problem is:

$$L(k, S, \lambda) = \sum_{0}^{T-1} \frac{1}{(1+r)^t}\left(R_t (P_x f(k_t) - P_E k_t)\right) + \frac{1}{(1+r)^T} G(R_T) + \sum_{0}^{T-1} \frac{1}{(1+r)^t} \lambda_t [R_t - R_t f(k_t) - S_t], \quad [1]$$

where $k = (k_0, \ldots, k_{T-1})$, $S = (S_0, \ldots, S_{T-1})$, and $\lambda = (\lambda_0, \ldots, \lambda_{T-1})$, and R_0 is given.

The appropriate Kuhn-Tucker necessary conditions for a maximum of $L(k, S, \lambda)$ are as follows:

$$\partial L/\partial k_t \leqslant 0; k_t \partial L/\partial k_t = 0, \quad t = 0, \ldots, T-1; \quad [2]$$

$$\partial L/\partial S_t \leqslant 0; S_t \partial L/\partial S_t = 0, \quad t = 0, \ldots, T-1; \quad [3]$$

$$\partial L/\partial \lambda_t = 0, \quad t = 0, \ldots, T-1. \quad [4]$$

It is assumed that the solution to the maximizing problem is interior; i.e., $k_t > 0, S_t > 0, \lambda_t > 0$. Then [2] and [3] are satisfied if [5], [6], and [7] are true:

$$(P_x - \lambda_t)\, f'(k_t) = P_E, \quad t = 0, \ldots, T-1; \quad [5]$$

$$\lambda_{t-1} = \frac{1}{(1+r)} \left(P_x\, f(k_t) - P_E\, k_t\right) dR_t/dS_{t-1} + \frac{1}{(1+r)} \lambda_t\, [1 - f(k_t)]\, dR_t/dS_{t-1},$$

$$t = 1, \ldots, T-1; \quad [6]$$

$$\lambda_{T-1} = \frac{1}{(1+r)} \frac{dG}{dR_T} \frac{dR_T}{dS_{T-1}}, \quad [7]$$

and [4] is satisfied if [8] is true.

$$S_t = R_t - R_t\, f(k_t), \quad t = 0, \ldots, T-1. \quad [8]$$

For $t = 1$ equation [6] can be written more simply as

$$\lambda_0 = \frac{1}{1+r}[P_x\, f(k_1) - P_E\, k_1] \frac{dR_1}{dS_0} + \frac{1}{1+r} \lambda_1 \frac{\partial S_1}{\partial S_0}. \quad [6']$$

By substituting for λ_1 in [6'], an expression of λ_0 results with λ_2 in it, and by substituting for λ_2 an expression of λ_0 results with λ_3 in it, and so on until an expression of λ_0 results with λ_{T-1} in it. Equation [7] can then be substituted for λ_{T-1}.[6] The resulting expression is:

$$\lambda_0 = \sum_{t=1}^{T-1} \frac{1}{(1+r)^t} \left[P_x\, f(k_t) - P_E\, k_t\right] \frac{\partial R_t}{\partial S_0} + \frac{1}{(1+r)^T} \frac{dG}{dR_T} \frac{\partial R_T}{\partial S_0}. \quad [9]$$

Equation [5] can be rewritten for $t = 1$ as

$$\lambda_0 = P_x - P_E/f'(k_0). \quad [5']$$

Equation [5'] suggests that λ_0 can be interpreted as the marginal profitability of catching an additional fish in period 0, while equation [9] suggests that λ_0 can be interpreted as the present value of the marginal profitability of adding an additional spawner to the escapement level in period 0; i.e., the level of escapement should be selected in time period 0 such that the incremental profitability of an additional fish caught today is just equal to the present value of the profitability of the future return resulting from an incremental spawner. In order to attain the desired level of escapement it is necessary to select an appropriate level of k_0, since escapement is equal to the run size in period 0 minus the catch. Note that this analysis can be applied to any time period t, not just to $t = 0$.

In order for the analysis to be valid in the general form presented here, it is necessary to prove the existence of values for $k = (k_0, \ldots, k_{T-1})$, $S = (S_0, \ldots, S_{T-1})$, and $\lambda = (\lambda_0, \ldots, \lambda_{T-1})$, which satisfy equations [5], [6], [7], and [8] given $R_0 = R(0)$. This is not an easy task if T is finite, so it is assumed that $T \to \infty$.[7] In this situation an equilibrium, or steady state solution is possible, where

$$k^* = k_0 = k_1 = \ldots, = k_T$$

$$S^* = S_0 = S_1 = \ldots, = S_T$$

$$\lambda^* = \lambda_0 = \lambda_1 = \ldots, = \lambda_T.$$

If T is finite this kind of a solution makes no sense. If $T \to \infty$ and an equilibrium solution exists, then equation [9] can be rewritten as

[6] This procedure is discussed in Burt and Cummings (1970).

[7] For a discussion of the mathematical problems involved in the case of an infinite time horizon (Burt and Cummings, 1970).

$$\lambda^* = \sum_{t=1}^{\infty} \frac{1}{(1+r)^t} [P_x f(k^*) - P_E k^*] \frac{\partial R_t^*}{\partial S_0} + \lim_{T \to \infty} \frac{1}{(1+r)^T} \frac{dG}{dR_T} \frac{\partial R_T^*}{\partial S_0}.^{8} \quad [9']$$

Both expressions to the right of the equal sign in equation [9′] must converge for existence. This requires that

$$\frac{dR^*}{dS} [1 - f(k^*)] < 1 + r. \quad [10]$$

Then equation [9′] can be rewritten as

$$\lambda^* = \frac{1}{1+r} [P_x f(k^*) - P_E k^*] \frac{dR^*}{dS} \cdot \frac{1}{1 - \frac{[1-f(k^*)]}{1+r} \frac{dR^*}{dS}} \quad [9'']$$

since $\lim_{T \to \infty} \frac{1}{(1+r)^T} \frac{dG}{dR_T} \frac{\partial R_T^*}{\partial S_0}$ converges to zero for $\frac{dG}{dR_T}$ bounded. Also [5] and [8] can be rewritten as

$$(P_x - \lambda^*) f'(k^*) = P_E, \quad [5']$$

$$S^* = R^* - R^* f(k^*). \quad [8']$$

Equations [10] and [9″] together suggest that the productivity of the spawner stock in producing additional spawners must be less than the social rate of discount, r, in order for λ^*, the profitability of an incremental spawner, to be positive.

A steady state solution exists if the determinant of the Jacobian matrix for [5′], [8′], and [9″], is non-zero. It can be proven that the Jacobian determinant is negative if it is assumed that the expression to the left of the inequality sign in [10] is less than or equal to 1. Unfortunately, there is no reason to assume this, even though in the context of a specific model, with functions and parameters assigned, one might expect that it is true.[9]

Note that the equilibrium solution requires that $R_0 = S^*/(1 - f(k^*))$. Clearly there is no reason to anticipate that the initial run size will be at the desired level for an equilibrium solution, and to reach the desired level may be costly. Hence, the analysis ignores the question of optimal policy for reaching the equilibrium solution. Note also that there is no reason to anticipate that S^*, the equilibrium solution, will correspond to maximum sustained yield. These issues are discussed more extensively in the appendix in the context of a continuous time model.

MORE COMPLEX MODELS

A simple model of the type presented in the previous section is not completely realistic for certain species of salmon where fish spawned in time period t will return to their spawning grounds in time periods $t+4$, $t+5$, and $t+6$. Assuming that the percentages of the total return to the river in time periods $t+4$, $t+5$, and $t+6$ from spawning efforts in time period t are constants, a_4, a_5, and a_6, the spawner-return relationship becomes:

$$R_t = S_{t-4} a_4 a e^{(bS_{t-4})} + S_{t-5} a_5 a e^{(-bS_{t-5})} + S_{t-6} a_6 a e^{(-bS_{t-6})}, \quad [11]$$

where $a_4 + a_5 + a_6 = 1$.

[8] In a steady state solution,

$$\frac{\partial R_t}{\partial S_0} = \frac{dR^*}{dS} \left([1 - f(k^*)] \frac{dR^*}{dS} \right)^{t-1}$$

where * denotes evaluation at the equilibrium solution. Note also that

$$\frac{\partial R_t}{\partial S_1} = \frac{dR_t}{dS_{t-1}} \prod_{\tau=1}^{t-1} [1 - f(k_\tau)] \frac{dR_T}{dS_{\tau-1}} = \frac{dR_t}{dS_{t-1}} \prod_{\tau=1}^{t-1} \frac{\partial S_\tau}{\partial S_{\tau-1}}$$ in the general case.

[9] See the appendix for a proof that the Jacobian determinant is negative for the given assumption.

The Lagrangian for the maximizing problem now becomes:

$$L = \sum_{t=0}^{T-6} \frac{1}{(1+r)^t} \Big(R_t \left[P_x f(k_t) - P_E k_t \right] + \lambda_t \left[R_t - R_t f(k_t) - S_t \right] \Big) + \sum_{t=T-5}^{T} \frac{1}{(1+r)^t} G(R_t), \quad [12]$$

given $R(0) = R_0$, $R(1) = R_1$, $R(2) = R_2$, $R(3) = R_3$, $R(4) = R_4$, and $R(5) = R_5$. Note that in this model R_0, R_1, R_2, R_3, R_4, and R_5 are the given initial run sizes and that the terminal value condition must be modified to account for the more complex spawner-return relationship now being used. Also, it is implicitly assumed that run sizes in the last five periods have no direct effect on one another, but are determined by spawner stocks in previous periods. Once $T \to \infty$ is allowed this assumption becomes unimportant.

The necessary conditions for a maximum of L with $k_t > 0$, $S_t > 0$, $\lambda_t > 0$ are satisfied if:

$$(P_x - \lambda_t) f'(k_t) = P_E, \quad t = 0, \ldots, T-6; \quad [13]$$

$$\lambda_{t-4} = \frac{1}{(1+r)^4} \Big(\left[P_x f(k_t) - P_E k_t \right] + \lambda_t \left[1 - f(k_t) \right] \Big) \frac{\partial R_t}{\partial S_{t-4}} + \frac{1}{(1+r)^5} \Big(\left[P_x f(k_{t+1}) - P_E k_{t+1} \right] + \lambda_{t-1} \left[1 - f(k_{t+1}) \right] \Big) \frac{\partial R_{t+1}}{\partial S_{t-4}} + \frac{1}{(1+r)^6} \Big(\left[P_x f(k_{t+2}) - P_E k_{t+2} \right] + \lambda_{t-2} \left[1 - f(k_{t+2}) \right] \Big) \frac{\partial R_{t+2}}{\partial S_{t-4}},$$

$$t = 4, \ldots, T-8; \quad [14]$$

$$\lambda_{T-11} = \frac{1}{(1+r)^4} \Big(\left[P_x f(k_{T-7}) - P_E k_{T-7} \right] + \lambda_{T-7} \left[1 - f(k_{T-7}) \right] \Big) \frac{\partial R_{T-7}}{\partial S_{T-11}} + \frac{1}{(1+r)^5} \Big(\left[P_x f(k_{T-6}) - P_E k_{T-6} \right] + \lambda_{T-6} \left[1 - f(k_{T-6}) \right] \Big) \frac{\partial R_{T-6}}{\partial R_{T-11}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-5}} \frac{\partial R_{T-5}}{\partial S_{T-11}}; \quad [15]$$

$$\lambda_{T-10} = \frac{1}{(1+r)^4} \Big(\left[P_x f(k_{T-6}) - P_E k_{T-6} \right] + \lambda_{T-6} \left[1 - f(k_{T-6}) \right] \Big) \frac{\partial R_{T-6}}{\partial S_{T-10}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-5}} \frac{\partial R_{T-5}}{\partial S_{T-10}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-4}} \frac{\partial R_{T-4}}{\partial S_{T-10}}; \quad [16]$$

$$\lambda_{T-9} = \frac{1}{(1+r)^4} \frac{dG}{dR_{T-5}} \frac{\partial R_{T-5}}{\partial S_{T-9}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-4}} \frac{\partial R_{T-4}}{\partial S_{T-9}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-3}} \frac{\partial R_{T-3}}{\partial S_{T-9}}; \quad [17]$$

$$\lambda_{T-8} = \frac{1}{(1+r)^4} \frac{dG}{dR_{T-4}} \frac{\partial R_{T-4}}{\partial S_{T-8}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-3}} \frac{\partial R_{T-3}}{\partial S_{T-8}} + \frac{1}{(1+r)^6} \frac{dG}{dR_{T-2}} \frac{\partial R_{T-2}}{\partial S_{T-8}}; \quad [18]$$

$$\lambda_{T-7} = \frac{1}{(1+r)^4} \frac{dG}{dR_{T-3}} \frac{\partial R_{T-3}}{\partial S_{T-7}} + \frac{1}{(1+r)^5} \frac{dG}{dR_{T-2}} \frac{\partial R_{T-2}}{\partial S_{T-7}}$$

$$+\frac{1}{(1+r)^6}\frac{dG}{dR_{T-1}}\frac{\partial R_{T-1}}{\partial S_{T-7}}\ ; \qquad [19]$$

$$\lambda_{T-6} = \frac{1}{(1+r)^4}\frac{dG}{dR_{T-2}}\frac{\partial R_{T-2}}{\partial S_{T-6}} + \frac{1}{(1+r)^5}\frac{dG}{dR_{T-1}}\frac{\partial R_{T-1}}{\partial S_{T-6}} + \frac{1}{(1+r)^6}\frac{dG}{dR_T}\frac{\partial R_T}{\partial S_{T-6}}\ ; \qquad [20]$$

$$S_t = R_t[1-f(k_t)], t=0,\ldots,T-6. \qquad [21]$$

For a steady state (k^*, S^*, λ^*) these necessary conditions reduce to the following:

$$(P_x-\lambda^*)\,f'(k^*) = P_E, \qquad [22]$$

$$\lambda^* = [P_x f(k^*) - P_E k^*]\frac{dR^*}{dS} \times \frac{D}{1-D[1-f(k^*)]\frac{dR^*}{dS}} \qquad [23]$$

$$S^* = R^*[1-f(k^*)], \qquad [24]$$

where $D = \frac{a_4}{(1+r)^4}+\frac{a_5}{(1+r)^5}+\frac{a_6}{(1+r)^6}$.

In order for λ^* to be positive, $[1-f(k^*)]\frac{dR^*}{dS}$ must be less than $1/D$. The economic interpretations of [22], [23], and [24] are the same as the corresponding interpretations of [5′], [9″], and [8′] in the second section.

Some biologists believe that for certain species and spawning grounds spawned salmon in time period t will deplete the spawning grounds of food to such a degree that food sources will not be replenished sufficiently in time period $t+1$ to support an equally large number of spawned fish. The nature of this phenomenon has not yet been very well specified, but one possible expression of it is the following spawner-return relationship where feeding interaction between years is accounted for by modification of the power term for e:

$$R_t = S_{t-4}\,a_4 a e^{(-b_1S_{t-4}-\,b_2S_{t-5})} + S_{t-5}\,a_5 a e^{(-b_1S_{t-5}-\,b_2S_{t-6})} + S_{t-6}\,a_6 a e^{(-b_1S_{t-6}-\,b_2S_{t-7})}\ . \qquad [25]$$

The necessary conditions in a steady state for the model using this spawner-return relationship are the same as [22], [23], and [24], except that $\frac{dR^*}{dS}$ must be replaced by

$$\frac{dR^*}{dS} = ae^{-(b_1+\,b_2)S^*}\,(1-b_1S^* - \frac{b_2}{1+r}\,S^*).$$

One thing should be noted about the two models presented in this section. In order to attain the steady state solution, it is necessary to set the run size equal to its equilibrium solution level for the first six periods in the first model and the first seven periods in the second model. Hence, the problem of attaining the equilibrium solution is of greater magnitude here than in the simple model, where it was necessary to set the run size equal to its equilibrium solution level only in the initial period. This problem can, perhaps, be more adequately dealt with in the framework of a specific model and, in any case, requires further research.

NEEDED REFINEMENTS

Thus far, the analysis considers only necessary conditions for the existence of a maximizing solution. Sufficient conditions for existence are satisfied if the Lagrangian is concave in all variables. Unfortunately, concavity neither can be proved or disproved for the models examined in this paper. Again, the proof may be possible in the context of a more specific model, where all parameters and functions are assigned.

A practical application of the model presented here would involve significantly difficult estimation problems. Some work has already been done on estimating spawner-return functions, but the results in most cases have not been too promising (Mathews, 1967). The spawner-re-

turn relationships seem to possess a high degree of variability, which suggests that a stochastic specification of the problem may be more realistic than our deterministic approach. Estimating a catch function may also be troublesome since it would require a careful specification of effort and of its price.

Despite the difficulties, construction of a working model would be worthwhile because it would provide insight into some of the unresolved mathematical problems mentioned above, and more importantly it would provide further information on the significance of the difference between the magnitude of spawner stocks selected on the basis of maximum sustained yield and stocks selected on the basis of economic optimality as defined in this paper.

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APPENDIX

A continuous time analog to the simple model will now be discussed briefly. The problem is to maximize.

$$\int_0^\infty R_t[P_x f(k_t) - P_E k_t] e^{-\rho t} dt \qquad [A\text{-}1]$$

subject to

$$\dot{S}_t = R_t[1 - f(k_t)] - S_t, \qquad [A\text{-}2]$$

where $\dot{S}_t = \frac{dS_t}{dt}$, and ρ is the continuous time discount rate. The appropriate Hamiltonian for the maximum problem is

$$H = e^{-\rho t}\Big(R_t[P_x f(k_t) - P_E k_t] + \lambda_t[R_t[1\text{-}f(k_t)] - S_t - \dot{S}_t]\Big). \qquad [A\text{-}3]$$

Assuming the existence of an interior solution, the necessary conditions for a maximum are, along with [A-2],

$$\frac{\partial H}{\partial k_t} = 0, \qquad [A\text{-}4]$$

$$\frac{d}{dt}\frac{\partial H}{\partial S_t} = \frac{\partial H}{\partial S_t}. \qquad [A\text{-}5]$$

[A-4] and [A-5] are satisfied if

$$(P_x - \lambda_t) f' = P_E, \qquad [A\text{-}4']$$

$$\dot{\lambda}_t = \rho\lambda_t - \Big([P_x f(k_t) - P_E k_t] \frac{dR_t}{dS_t} + \lambda_t[1 - f(k_t)] \frac{dR_t}{dS_t} - \lambda_t \Big) \qquad [A\text{-}5']$$

where $\dot{\lambda}_t = d\lambda/dt$.

If [A-4'] is used to eliminate one of the unknowns, the result is a system of two differential equations in two unknowns, [A-2] and

[A-5']. Utilizing the following derivatives, it is possible to consider a phase diagram analysis of this equation system.

$$d\lambda_t/dS_t \Big|_{\dot{\lambda} = 0} =$$

$$+\left(\frac{[P_x f(k_t) - P_E k_t] + \lambda_t[1 - f(k_t)]}{\rho + 1 - [1 - f(k_t)]\, dR_t/dS_t} \right) \frac{d^2R_t}{dS_t^2} \qquad \text{[A-6]}$$

$$d\lambda_t/dS_t \Big|_{\dot{S} = 0} =$$

$$\frac{(P_x - \lambda_t) f'' \left([1 - f(k_t)] \frac{dR_t}{dS_t} - 1 \right)}{R_t f'^2}, \qquad \text{[A-7]}$$

$$\frac{\dot{d\lambda}}{dS_t} \Big|_{\lambda \text{ constant}} =$$

$$-\left([P_x f(k_t) - P_E k_t] + \lambda_t[1 - f(k_t)] \right) \frac{d^2R_t}{dS_t^2}, \qquad \text{[A-8]}$$

$$\frac{\dot{dS}}{d\lambda_t} \Big|_{S_t \text{ constant}} = -\frac{R_t f'(k_t^2)}{(P_x - \lambda_t) f''(k_t)}. \qquad \text{[A-9]}$$

Before proceeding with the analysis, note that:

(i) $f' > 0, f'' < 0, P_x - \lambda_t > 0$ by [A-4'], and $[(P_x - \lambda_t) f(k_t) - P_E k_t + \lambda_t] > 0$ since $P_x - \lambda_t = P_E/f'$ and $f > f' k_t$.

(ii) If a steady state solution exists, such that $\dot{\lambda}_t = 0$ and $\dot{S}_t = 0$, which satisfies the necessary conditions for a maximum, the equilibrium value for S_t, S^*, will be such that $S^* \leqslant \bar{S}_t$ where $\bar{S}_t$ maximizes R_t as a function of S_t. The reason for this was discussed in the section on Notation and Assumptions. It then follows that $dR_t/dS_t > 0$, and $d^2R_t/dS_t^2 < 0$.

(iii) $0 < [1 - f(k_t)] \leqslant 1$ since $S_t = R_t\,[1 - f(k_t] \geqslant 0$ and $S_t \leqslant R_t$.

(iv) $dR_t/dS_t = 1$ evaluated at S_t^0, where S_t^0 is the spawner stock required for maximum sustained yield; if $S_t < S_t^0$, $dR_t/dS_t > 1$, and if $S_t > S_t^0$, $dR_t/dS_t < 1$.

It is now possible to attach signs to [A-6] through [A-8] as follows:

$$d\lambda_t/dS_t \Big|_{\dot{\lambda} = 0} < 0 \text{ for } S_t^0 \leqslant S_t \leqslant \bar{S}_t, \qquad \text{[A-10]}$$

indeterminant for $S_t < S_t^0$;

$$d\lambda_t/dS_t \Big|_{\dot{S} = 0} > 0 \text{ for } S_t^0 \leqslant S_t \leqslant \bar{S}_t, \qquad \text{[A-11]}$$

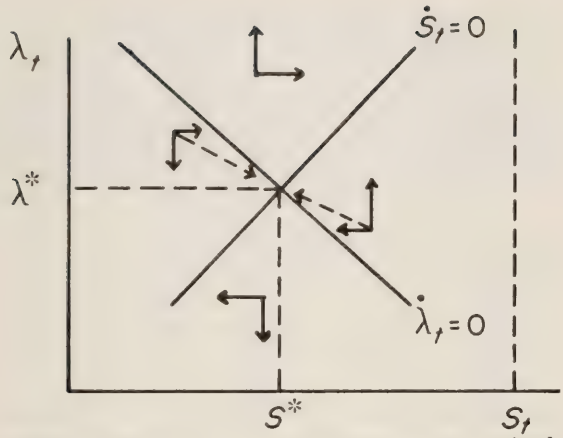
interminant for $S_t < S_t^0$;

$$\frac{\dot{d\lambda}}{dS_t} \Big|_{\lambda \text{ constant}} > 0 \text{ for } S_t \leqslant S_t. \qquad \text{[A-12]}$$

$$\frac{\dot{dS}}{d\lambda_t} \Big|_{S_t \text{ constant}} > 0, \ \forall\ S_t. \qquad \text{[A-13]}$$

If $[1 - f(k_t)]\, \frac{dR_t}{dS_t} \leqslant 1$, then there are no sign ambiguities in the relevant range, and the equilibrium solution exists. From the phase diagram in Appendix Figure 1, it is clear that the equilibrium is a saddle point; i.e., given an initial $S_0 \leqslant \bar{S}_t$, there exists a time path for λ_t, k_t, and S_t converging to the steady state equilibrium, along which the necessary conditions for a maximum are satisfied. Hence, the optimal policy for reaching a steady state solution can be specified even if $S_0 \neq S^*$. Again there is no reason for $S^* = S_t^0$, where S_t^0 corresponds to maximum sustained yield.

It is now possible to calculate the Jacobian determinant J of the system of equations [A-2] and [A-5'] evaluated at the steady state equilibrium, using [A-4'] to eliminate one of the variables. In order to calculate the determinant, the following derivatives are required:



APPENDIX FIGURE 1.—A phase diagram of optimal solution paths.

$$\frac{\partial \dot{\lambda}_t}{\partial \lambda_t} = \rho + 1 - [1 - f(k_t)]\, dR_t/dS_t, \quad \text{[A-14]}$$

$$\partial \dot{S}_t/\partial S_t = \frac{dR_t}{dS_t} 1 - f(k_t)] - 1. \quad \text{[A-15]}$$

Using [A-8], [A-9], [A-14], and [A-15], and assuming that $[1 - f(k_t)]\, \frac{dR_t}{dS_t} \leqslant 1$,

$$J = \begin{vmatrix} \frac{\partial \dot{\lambda}_t}{\partial \lambda_t} & \frac{\partial \dot{\lambda}_t}{\partial S_t} \\ \frac{\partial \dot{S}_t}{\partial \lambda_t} & \frac{\partial \dot{S}_t}{\partial S_t} \end{vmatrix} < 0.$$

If r is substituted for ρ in the determinant, it equivalent to the one discussed in the second section.

As in the second section, it is not possible to prove that the equilibrium solution satisfies sufficient conditions for a maximum, since, in this case, it is not possible either to prove or disprove the concavity of the Hamiltonian.

NOTES

A SECOND RECORD OF A RARE SIPHONOPHORE *EPIBULIA RITTERIANA* HAECKEL 1888

During a survey by the National Marine Fisheries Service research vessel *David Starr Jordan*, a siphonophore, *Epibulia ritteriana* Haeckel, of the family Epibuliidae, was collected in a neuston haul on July 10, 1971, at 0225 to 0246 hr, PST, in the northeast Pacific Ocean at lat 37°20′N, long 135°00′W. The only other record of this species was one specimen, described by Haeckel (1888), collected off Ceylon in 1882 during the *Challenger* Expedition. Evidence of the world-wide distribution is typical of most species of siphonophores.

Haeckel's identification was refuted by Totton and Bargmann (1965) who stated several reasons for their disagreement, the most important being that Haeckel had described a ring of palpons under the float which they said was a character not typical of the suborder Cystonectae. Totton and Bargmann (1965) stated further that the suborder included only the families Physalidae and Rhizophysidae; the Epibuliidae were considered "species inquirendae." They concluded that Haeckel's description was based on "an incompletely examined specimen of *Athorybia rosacea*," and "that Haeckel's figure is unrealistic and idealized though beautifully executed," and in their opinion, "if such animals existed no doubt one will be found again." They also disagreed with unillustrated descriptions of two species of Epibuliidae, one *Rhyzophysa chamissomis* by Eysenhardt (1821) and the other *Epibulia erythrophysa* by Brandt (1835). It was my good fortune to collect and observe the living cystonect, described and illustrated here, which I have identified as *E. ritteriana* by reference to Haeckel's drawings and description. Haeckel's specimen is identical with mine, except that the gastrozoids in his illustration have larger and more conspicuous mouths. I have also collected specimens of *Athorybia rosacea*, identified by direct observation and comparison with drawings by Totton and Bargmann (1965). Outstanding characters of *A. rosacea* are the shape of the pneumatophore and large and distinct bracts arranged in several layers. My specimen of *E. ritteriana* showed no evidence of bracts, nor scars or spaces where bracts could be attached. I believe, therefore, that the two species are not to be confused and that *Epibulia* does in fact exist, *ergo*, the family Epibuliidae.

The rarity of records for this family of cystonects may be attributed in part to the fact that as surface floating organisms they exist in a stratum seldom sampled by plankton tows because most "net time" is subsurface.

Description of *Epibulia ritteriana*

The complete corm of this Cystonectae is about 25 mm high and 20 mm in diameter, after preserved in 5% solution of formaldehyde (Figure 1). The whole colony presented brilliant shades of pink. The large ovate, almost spheric pneumatophore was coral red (light red) with the apical pore (with a sphincter) surrounded by a purple pigmentation, still visible after preservation. The crown of palpons around the float (young gastrozoids) and the siphons (gastrozoids) appeared rose, and the latter presented a purple spot near the end. Tentacles and tentilla were yellowish, the gonodendra bright red and purple.

The colony appears arranged as follows: pneumatophore and siphosome. The siphosome presents the palpons at the part closer to the pneumatophore, and the siphons at the other end, with the tentacles attached at the base; and the gonodendra distributed between the siphons.

The pneumatophore or top float is filled with gas, probably carbon monoxide as it is the case in other siphonophores (Pickwell, Barham, and Wilton, 1964). The pneumatophore is an ovate chitinous case, 8 mm × 10 mm in size. According to Haeckel (1888) the size of the pneumatophore ranged from 10 mm × 12 mm in the expanded stage to a spheroid of 3 to 4 mm after

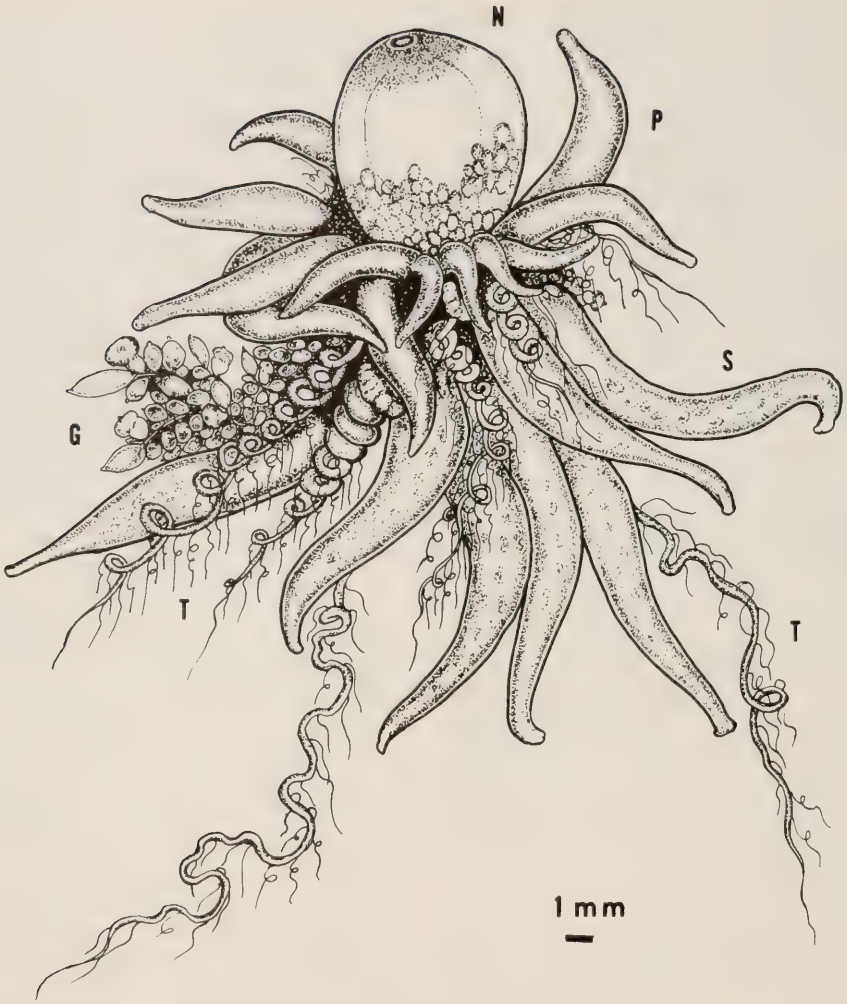


FIGURE 1.—*Epibulia ritteriana* Haeckel (1888), drawn from the specimen described in this paper. Key to the above is: N - pneumatophore, P - palpons, S - siphons or gastrozoids, T - tentacles with the tentilla, G - gonodendra.

the emission of the gas through the apical pore. The structure of the pneumatophore, according to Haeckel (1888) includes the pneumatocodon or outer wall of the pneumatophore, which is separated from the inner wall, or pneumatosac, pneumatocyst or air sac, which contains the gas gland; and the hypocystic villi (giant cells) protrude from the air sac into the pericystic space. The apical pore is closed by the stigmatis sphicter (ring muscle).

The siphosome is a short cone or ovate bladder, coiled, which Haeckel (1888) described as the "dexiotropic turning of a spire."

The palpons (feelers or tasters) are slender, cylindrical tubes, smaller than the siphons, with a thick muscular wall. They connect into the vascular trunk, and the outer end is armed with cnidocysts. The palpons are consequently then both sensory and protective organs.

The siphons or gastrozoids are large feeding polyps, 15 mm to 20 mm long, rod-shaped tubes of thick muscular wall. The largest part is the stomach with the hepatic villi, and the outer opening a muscular proboscis. The opening of the mouth may be expanded in a kind of disc or sucker, divided into several lobes. Haeckel's illustrations (1888) presented the gastrozoids with extremely large and expanded mouth. A long single contractile tentacle is attached at the base of each siphon.

The tentacle arising from the base of each gastrozoid consists of a long cylindrical tube reaching to 80 mm or more than 100 mm long when fully extended. The tentacles are long, contractile, and branched along their whole length, which is covered laterally by the single branched tentilla. The tentilla are short, thin, contractile filaments. Both tentacles and tentilla are covered with nematocysts. The concave side of each tentillum has sensitive papillae, and the convex side is armed with cnidocysts. Twisted masses of tentacles and tentilla form thick bunches, difficult to disentangle.

The gonodendra are attached by a short pedicle to the periphery of the vesicular trunk, between the palpons and the siphons or gastrozoids. The gonostyle is branched, and each branch has at the end a gonopalpon and a medusoid gynophore (female gonophore) and below a bunch of roundish androphores (male gonophores) resembling altogether miniature clusters of grapes.

Epibuliidae float at the surface of the waters, using the pneumatophore, swimming mainly by the coordinated movements of the palpons, and siphons. *E. ritteriana* adopts a vertical position in the water, and the colony drifts and twists at the surface of the sea, with the pneumatophore at the top, floating at the surface, and the tentacles shortened or extended deep into the waters like fishing lines, with the gastrozoids actively searching for food.

It is possible that *Cystalia monogastrica* Haeckel (1888) may be a juvenile stage of *Epibulia ritteriana.*

The scarcity of *E. ritteriana* is probably only apparent, due to the factors previously explained. Studies on the distribution of these highly predatory animals would be of interest, when related to the distribution of some fish larvae. These Cystonectae may feed voraciously on epiplanktonic animals, mainly on those inhabiting the uppermost layers of the epiplanktonic domain (Clupeidae, Engraulidae, and other fish larvae), which would suffer heavily under this active predation.

Acknowledgments

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DEEP OBSERVATIONS OF ANCHOVY AND BLUE SHARKS FROM *DEEPSTAR 4000*

Visual observations from manned deep-submersibles have recently contributed to the knowledge of the vertical distribution of marine organisms. Prior to the introduction of these craft, vertical distribution patterns were established using sampling gear such as nets. This was generally sufficient in the case of the smaller, easily captured forms since many of the nets used in these studies could be opened and closed at predetermined depths so that selected strata would be sampled exclusively. In the case of the larger, more active fishes, however, knowledge of their depth ranges has been mostly speculative. Sampling of these animals has normally been accomplished using commercial fishing gear which is generally indiscriminate with respect to the depth of capture. This has been true of the two species in question, the northern anchovy, *Engraulis mordax* Girard, and the blue shark, *Prionace glauca* (Linnaeus).

One method used to establish the depth of anchovy schools has been to locate them with echo sounders during the day when they are deep, then remain over them until they rise to the surface at night. Once the schools are at the surface, identification can be made with midwater trawls. Common daytime depths of these schools are between 140 and 220 m (personal communication with K. F. Mais, California Department of Fish and Game). Information on vertical distribution of blue sharks has been reported by Strasburg (1958). Analysis of longline fishing data from the central Pacific showed that these sharks were often captured on the deepest hooks. Although the exact depth of the hooks at the time of capture was not known, the approximate depths were in the 110-150 m range. This report, then, should serve as a visual verification of this previous information.

Dive 502 of the submersible *Deepstar 4000* was made on 9 November 1968 at lat 32°26'N, long 117°23'W, west of the Coronado Islands. On the way to the dive site from San Diego aboard the mothership *Searchtide*, a continuous echogram was made on a Gifft GDR-T depth recorder[1] driving a hull-mounted UQN-1 transducer at 12 kHz. Shortly after cresting the Coronado Escarpment, where the bottom dropped off to the deeper water of the San Diego Trough, hyperbolic targets appeared in the 160 to 270 m region of the recording. Underway at 12 knots, the largest of these had dimensions of 600 m horizontally, and 70 m vertically. As *Searchtide* hove-to at the dive site, these targets appeared as in Figure 1. Interspersed with the large targets were several discrete targets which appear on the record as lines, rather than large masses. The bottom depth at the site was approximately 1,200 m and its trace was programmed out of the recording.

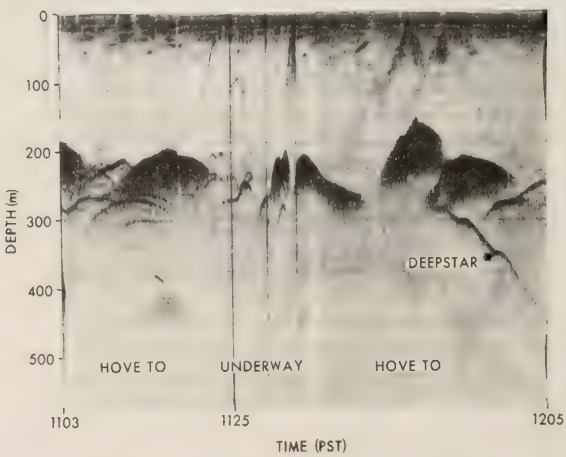

FIGURE 1.—Echogram recorded during *Deepstar* dive 502. The large targets between 150 and 250 m were observed to be schools of anchovy. The discrete traces may have been blue sharks. During the underway portion, the ship was repositioning over the submersible for tracking purposes. The acoustic return from *Deepstar*, a 2-m-diameter sphere, is labeled to provide a qualitative comparison of acoustic reflection strength.

The dive began at 1103 (PST), and a slow descent (13 m/min) was made to 100 m where two blue sharks were observed. This shark is a common species which is easily identified vis-

[1] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

ually. They swam actively out of the gloom, then veered away and circled for a short time before disappearing.

Continuing the descent, at approximately 180 m we became aware of the presence of a large concentration of fish at the periphery of the light field. The descent was stopped and we maneuvered in an attempt to obtain visual and photographic data. Each time the propulsion motors were activated, the fish would hurriedly retreat from view. Their movements were as a disciplined school. Several times we approached the school with the lights out, a technique which enabled the submersible *Alvin* to penetrate schools of myctophids in the Atlantic (Backus et al., 1968). Although we were never able to penetrate the school, the darkened submersible apparently attracted a few individuals who remained near the windows when the lights were switched on. Stunned by the sudden illumination, they remained transfixed long enough for good visual identification. The northern anchovy, with its projecting snout and thin body, is sufficiently distinct from other local clupeoids to give us confidence in our identification. Unfortunately, the photographs taken were blurred.

Three more blue sharks were observed at the same depth as the anchovy school. The deepest sighting was at 275 m. Because these were observed individually, the sightings could all have been of the same individual. Possibly, one of the same sharks sighted at 100 m may have followed *Deepstar* during the descent. We also observed a few squid, presumed to be *Loligo opalescens*, at the depth of the school. The spatial proximity of the sharks, squid, and anchovy suggests a predator-prey relationship, although no predation was observed.

The lower limit of the anchovy school was at 310 m and after dropping below it we descended to 590 m. There we released the descent weight and rose rapidly to the surface. The school was observed between 300 and 200 m during the ascent. The dive ended at 1407.

There is little doubt of the relationship between the anchovies and the large targets on the recording. It is difficult, however, to be sure that there is a correlation between the sharks and the discrete targets. Whatever is responsible for these traces has a high acoustic target strength at 12 kHz. This can be seen by comparison on the figure with the trace made by *Deepstar*, a 2-m-diameter air-filled sphere.

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THE USE OF CONCENTRATION INDICES IN FISHERIES [1, 2]

The temporal-spatial distribution of organisms has generated considerable interest among biologists. This interest has generated many studies which deal primarily with the distribution of a single organism in space. In this note we consider the relationship between two organisms in space or time. We are interested, in particular, in an index of the relation between a predator (a fishing fleet) and a prey (the population to be harvested). We begin by writing

[1] Quantitative Science Paper No. 12. This series is prepared under the general sponsorship of the Quantitative Ecology and Natural Resource Management Program supported by Ford Foundation Grant Number 68-183.

[2] Portions of this study were undertaken while B. J. Rothschild was affiliated with the Center for Quantitative Science in Forestry, Fisheries, and Wildlife, University of Washington, Seattle.

the concentration index, suggested by Gulland (1955), which is the ratio of the ratio of averages catch-per-unit-of-effort statistic to the average of ratios catch-per-unit-of-effort statistic,

$$I_g = [\frac{\Sigma c}{\Sigma f}] \ [\frac{1}{n}\Sigma\frac{c}{f}]^{-1} \qquad (1)$$

where the c denotes catch and the f denotes effort and the summations can extend over either space or time. The index I_g has appeared in many fishery papers such as, for example, Paloheimo and Dickie (1964), Calkins (1963), etc. We can see that when $I_g > 1$, the fishermen tend to be concentrating on the fish, when $I_g < 1$, the fishermen tend to be fishing where the fish are *not* most abundant, and when $I_g = 1$, there is no relation between the distribution of fish and fishermen. It might be mentioned, somewhat parenthetically, that the situation where $I_g < 1$ is rather unusual for single species fisheries, but possible in mixed species fisheries when computed for a single species that is not the main object of the fishery.

Now we observe that when the numerator and denominator of (1) are equal (that is, there is no relation between the distribution of the fish and the fishermen), we can write

$$\frac{\frac{1}{n}\Sigma c}{\frac{1}{n}\Sigma f} - \frac{1}{n}\Sigma\frac{c}{f} = 0 \qquad (2)$$

Now multiply both sides of (2) by $\frac{1}{n}\Sigma f$ and note that whenever we sum a term and multiply by $\frac{1}{n}$ we have the average value of that term which we denote by the operator E, and so (2) becomes

$$E(c) - E(\frac{c}{f})E(f) \qquad (3)$$

which is, by definition, the covariance between catch-per-unit-of-effort and effort. It follows then that when the numerator and denominator (the two bracketed terms in (1)) are equal and (2) holds, then (3) must also equal zero, implying that when there is no relation between the distribution of fishermen and fish as indicated by the equality of the numerator and denominator in (1), the covariance between catch-per-unit-of-effort and effort is zero, and hence the correlation between catch-per-unit-of-effort and effort is also zero.

The difficulty with (1) is that it provides an index that is conceptually difficult to interpret, does not contain all of the information that is in the data, is asymmetrical about the point $I_g = 1$, and has no upper bound. All of these difficulties can be alleviated by dividing the covariance in (3) by the geometric mean of the variances of c/f and f, yielding the correlation coefficient,

$$I_r = \frac{\frac{1}{n}\Sigma c - \frac{1}{n}\Sigma\frac{c}{f}\cdot\frac{1}{n}\Sigma f}{\sqrt{\widehat{var}\ (\frac{c}{f}) \cdot \widehat{var}\ (f)}} \qquad (4)$$

where $_{var}\ (c/f)$ and $_{var}\ (f)$ refer to the usual sample estimates of variance. Thus I_r will be centered on zero, bounded by —1 and 1. Positive values of I_r imply that high values of effort will be associated with high values of CPUE whereas negative values of I_r imply that high values of effort will be associated with low values of CPUE. When $I_r = 0$, CPUE is not correlated with effort, a condition which, as previously noted, is equivalent to $I_g = 1$.

The fact that I_r contains more information than I_g is demonstrated in the following example based on three contrived sets of data. These data are listed in Table 1 and depicted in Figure 1. We can see that the slopes of lines fitted to each of the three data sets are the same and that I_g for each data set is also the same, but that I_r is different for each data set measuring the variability in c/f for fixed f as well.

In many instances the region in time or space for which these indices are computed will contain relatively few, highly variable, observations. This situation, in particular, raises the question

TABLE 1.—Contrived data under conditions of low, intermediate and high variability which are used to demonstrate the indices I_g and I_r.

Low variability			Intermediate variability			High variability		
c	f	c/f	c	f	c/f	c	f	c/f
10	2	5	6	2	3	2	2	1
10	2	5	14	2	7	18	2	9
49	7	7	35	7	5	21	7	3
49	7	7	63	7	9	77	7	11
Σ 118	18	24	118	18	24	118	18	24
I_g	1.09			1.09			1.09	
I_r	1.00			0.55			0.44	

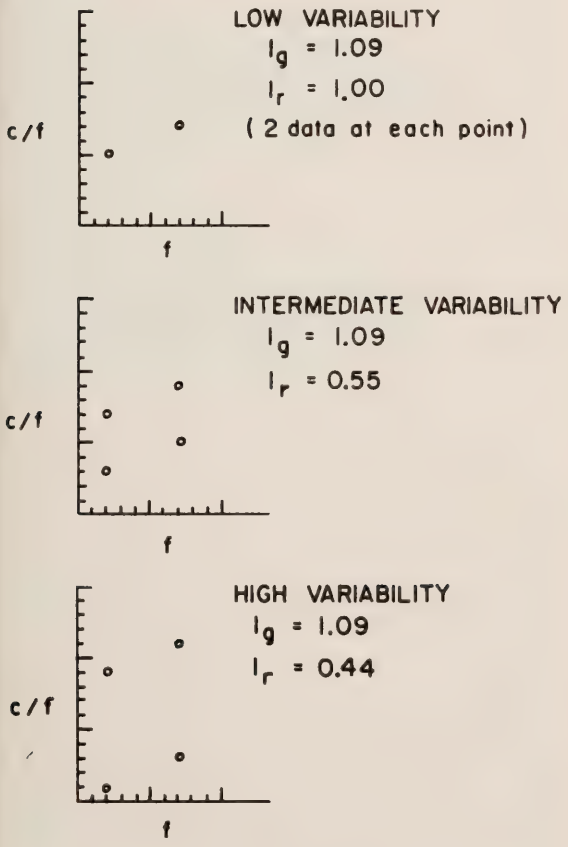

FIGURE 1.—Comparisons of I_g and I_r for c/f and f relations having different amounts of variability. The data are from Table 1.

of the amount of confidence that can be placed in any estimate of I_r or in I_g. The question of confidence can be resolved in the case of I_r if c/f and f are both drawn from the same (at least approximately) bivariate normal distribution. In the likely event that c/f and f are not at least approximately bivariate normal, then perhaps a transformation might be useful. It is also of interest to observe that since I_r is a correlation coefficient then we can interpret I_r^2 as the percentage of the total variability in c/f which is accounted for by regressing c/f upon f. Furthermore there is no reason, of course, why we could not extend this concept in multiple species fisheries to consider these sorts of data in a multiple correlation context.

The idea of using the correlation coefficient measuring the association between c/f and f as a concentration index is intuitively quite obvious and most likely would not be noteworthy except to call attention to the similarity to a commonly used index (I_g) which, in most instances, does not afford as large a scope for interpretation as does I_r. There are some cautions, however, which should be observed and these include, in addition to bivariate normality if we wish to construct confidence intervals, linearity in the relation between c/f and f. If, for example, the gear is saturated or data are pooled from various seasons, then linearity may not be a reasonable underlying model.

In the interpretation of either I_r or I_g it would be helpful to have auxiliary information because without this information it is impossible to determine whether increases in these indices result from an increased concentration of fishing on fish or fish on the location where fishermen happen to be fishing. Thus, these indices alone will not tell us whether changes in apparent abundance result from changes in actual abundance or changes in the skills of fishermen or both.

We should also draw attention to the fact that the relation of c/f and f is generally used in fisheries to determine "optimum" yield by regressing, usually annual, values of c/f upon f. This relation is frequently linear with a negative slope and is usually transformed into a parabolic function of c upon f indicating that level of f for which c is a maximum. The procedure outlined

has been criticized from a statistical point of view because c/f and f are obviously correlated. A measure of the magnitude of this correlation is clearly implied by (3) or (4).

Finally we should point out that our allusion to considering these indices as expressing relation among organisms was not careless because it seems to us that predator-prey relationships might be further elucidated through examination of concentration indices. For example, it would be interesting to relate the catch (in number of prey organisms) per predator stomach to the number of predator stomachs. This, however, is just a special case of the wealth of fishery-fish interaction models which could be applied to the prey-predator situation.

Acknowledgments

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SUITABILITY OF INTERNAL TAGS FOR ATLANTIC MENHADEN

Investigations of the Atlantic menhaden resource depend primarily on sampling and analyses of the commercial landings and studies of menhaden biology and ecology. Results of these studies give a broad understanding of the resource but sometimes lack the reliability of more direct evidence. Tagging and recovery of menhaden help provide the reliable information on movements, population size, availability, mortality, and growth rates required to better understand the resource.

The methods by which menhaden are caught, handled, and processed determine some of the requirements for tagging. Menhaden are captured in purse seines and are transferred by suction pumps from the nets to the vessels and from the vessels to the reduction plants. In the plant, the fish are cooked, pressed, dried, and ground into meal. From the time the fish are caught until they are processed into oil and meal, there is little opportunity to handle or see an individual menhaden. Consequently tags or tagged fish must be recovered by mechanical or electronic means. Internal ferromagnetic tags that are mechanically or electronically recoverable have been developed for Atlantic and Pacific herring, Pacific sardine, and anchoveta.

We conducted a series of experiments at Beaufort, N.C., to find a mark suitable for Atlantic menhaden. In 1959 we tagged young menhaden with a nickel-plated, steel tag, (Type A in Figure 1). The tagged menhaden died within a week, terminating the experiment. During 1960 we attempted to mark menhaden with fluorescent pigments and to develop a photoelectric detector. The occurrence of natural fluorescence in menhaden and other marine organisms made discrimination of marked fish impractical (Reintjes, 1963). In 1961-62 we resumed tests with internal tags to select a type suitable for menhaden and to demonstrate its recovery with magnets in a menhaden reduction plant.

Tagging Experiments and Tag Selection

We selected four ferromagnetic tags (Table 1 and Figure 1) for insertion in young Atlantic

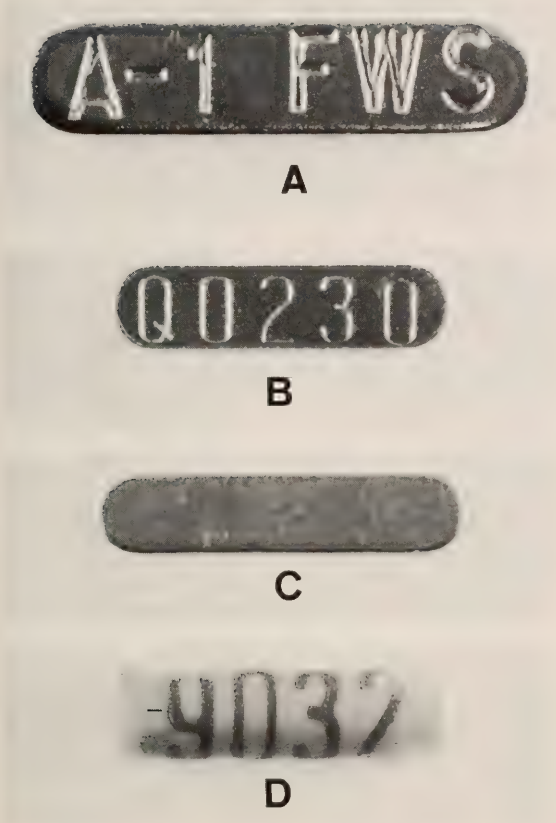

FIGURE 1.—Four ferromagnetic tags tested for marking Atlantic menhaden.

TABLE 1.—Four types of ferromagnetic tags tested for marking Atlantic menhaden.

Type	Materials	Dimensions	Weight	Shape
		mm	*g*	
A	Nickel-plated steel	19 × 4 × 1.5	0.89	rectangular
B	Nickel-plated steel	12.5 × 3 × 0.6	0.19	rectangular
C	Stainless steel	14 × 2.5 × 0.3	0.15	rectangular
D	Plastic capsule	12 × 3	0.63	cylindrical

menhaden. Type A tags were similar to tags used for Pacific herring (Rounsefell and Dahlgren, 1933) except were twice as thick and had sharp edges. Type B tags, also with sharp edges, were similar to tags used for California sardine (Janssen and Aplin, 1945), anchoveta (Bayliff and Klima, 1962) and anchovy (Vrooman, Paloma, and Jordán, 1966; Haugen, Messersmith, and Wickwire, 1969; Wood and Collins, 1969). Type C tags were similar to tags used for small Atlantic herring in Norway (Dragesund and Hognestad, 1960) and had smooth edges. Type D tags, used for Pacific herring (Wilimovsky, 1963), were dummy radioactive tags that consisted of a gold-plated iron core encased in plastic.

Young menhaden, 115-168 mm fork length, were caught nearby and held in concrete tanks at the laboratory for several weeks prior to the tagging trials. They were fed a homogenized slurry of fish meal and raw hard clams throughout confinement. Test lots of menhaden for each tag type consisted of equal numbers of tagged, incised but not tagged, and handled but not incised or tagged. A fifth lot of fish, not handled, was used as controls.

At tagging, menhaden were transferred to a tank of seawater containing 50 ppm tricaine methanesulfonate (MS-222) until they lost equilibrium. With a scalpel a technician made a small incision on the right side below the midline of the body about midway between the tip of the pectoral fin and the insertion of the pelvic fins to minimize disturbance of viscera. He inserted metal tag Type A, B, or C, into the body with forceps (Figure 2) and Type D through a hollow needle.

The tags and instruments were dipped in a mixture of penicillin G and liquid terramycin. These antibiotics were also added to the anesthetizing tank. All fish were hand-held for 20 sec whether they were tagged, incised, or only handled.

Dead fish and shed tags were removed daily. The dead were measured, weighed, and examined for abnormalities by X-ray and by dissection. The study was concluded in January 1962 when the temperature in the tanks dropped overnight from 3.0° to 0.4°C and most of the fish died. During the preceding 10 weeks the water had cooled gradually from 22°C without killing the fish. Salinity, during this period, ranged from 27 to 32‰.

The Norwegian herring tag, Type C, was the most suitable of the four tested. Tag D was not considered further for it cost ten times more

than the metal tags, and we were not planning to use its radioactive capability.

The numbers of menhaden that died in each tagging experiment are shown in Table 2. Tag Type A caused the most deaths. The combined loss from dying and shedding are shown in Table 3. More menhaden tagged with Types A and B died or shed their tags than did those with Type C. From these trials, Type C was selected for menhaden tagging studies.

Menhaden that died during the experiment and those that survived until the end of the 10-week period were examined for an apparent cause of death. At the end of the 10-week period, all survivors had healed incisions that were faintly visible as slight depressions without scales. Recipients of Type A tags dying during the study had enlarged open wounds and some tags protruded. Types A and B tags found in dead fish or loose on the bottom of the tanks were corroded. The peritoneum did not heal in any incised fish. Muscles were discolored near Types A, B, and D tags, and the tags were imbedded in the mesenteries near the cardiac and pyloric stomachs. Types A and B tags usually were enveloped with tissue. Types C and D tags were better for they apparently caused less irritation.

We were unsuccessful in our attempts to tag smaller menhaden, 75 to 90 mm fork length, in

TABLE 2.—Number of dead Atlantic menhaden in each tagging experiment at the end of 5 biweekly periods. [Number of fish in each lot in parentheses.]

	Number of weeks					
Tag type	2	4	6	8	10	Total
A						
Tagged (86)	1	3	6	2	0	12
Incised only (86)	1	1	0	0	0	2
Handled only (86)	0	1	1	0	0	2
B						
Tagged (86)	2	0	0	0	0	2
Incised only (86)	0	1	0	0	0	1
Handled only (86)	1	2	1	0	0	4
C						
Tagged (86)	1	1	0	0	0	2
Incised only (86)	0	0	0	0	0	0
Handled only (86)	1	1	0	0	0	2
D						
Tagged (33)	0	0	1	0	0	1
Incised only (33)	0	0	0	0	0	0
Handled only (83)	0	1	0	0	0	1
Controls (135)	2	1	0	0	0	3

TABLE 3.—Number of tags lost from experimental groups by death and shedding at the end of 5 biweekly periods. [Number of fish in each group in parentheses.]

	Number of weeks					
Tag type	2	4	6	8	10	Total
A (86)						
Dead	1	3	6	2	0	12
Shed	1	2	2	1	1	7
Total	2	5	8	3	1	19
B (86)						
Dead	2	0	0	0	0	2
Shed	8	2	0	2	2	14
Total	10	2	0	2	2	16
C (86)						
Dead	1	1	0	0	0	2
Shed	0	0	0	0	0	0
Total	1	1	0	0	0	2
D (33)						
Dead	0	0	1	0	0	1
Shed	0	0	0	1	1	2
Total	0	0	1	1	1	3

FIGURE 2.—Inserting a metal tag into the body cavity of young Atlantic menhaden.

August 1962. We used Type C tags but nearly all fish died within 5 days irrespective of treatment. Water temperatures over 30°C were partly responsible for the deaths. No more small menhaden were tagged.

Tag Recovery Trials

We tested the effectiveness of magnets to collect Type C tags in the menhaden reduction plants. Magnets usually are installed in plant conveyor systems to protect the hammermills from stray ferrous metal that breaks off machinery in the plant or is brought in with the fish. Menhaden are cooked and pressed, and the presscake is dried in rotary driers. Most of the dried scrap is pulverized into meal with hammermills.

In the first trial we tagged 102 dead menhaden in the storage or raw box and recovered 60 tags. Nine tags were retrieved from the magnet located after the drier within 8 hr, and the other 51 were collected on a second magnet several days later when the dried scrap was ground into meal (Table 4).

TABLE 4.—Recoveries of 340 tags released in a menhaden reduction plant.

Location and method of release	Number released	Number recovered	Recovery location		Total
			Magnet after drier	Magnet before hammermill	
			%	%	%
Raw box, in fish	102	60	9	50	59
Raw box, in fish	38	26	5	63	68
Cooker input, loose	40	26	12	53	65
Press input, loose	40	35	10	78	88
Press output, loose	40	33	17	65	82
Drier output, loose	40	34	18	67	85
Shed floor, loose	40	34	0	85	85

In the second trial, 238 tags were placed in different locations throughout the plant. Thirty-eight were placed in dead fish in the raw box, and five lots of 40 tags each were scattered loosely in (1) cooker, (2) press input, (3) press output, (4) drier output, and (5) storage shed floor. The recoveries ranged from 65 to 88%. These results showed that recovery of tags was practical with magnets already installed in menhaden plants. We believe the recovery efficiency could be improved by installing additional magnets in the processing system.

We concluded from these preliminary experiments that Atlantic menhaden longer than 115 mm fork length could be tagged internally with a smooth piece of stainless steel and that the tags could be recovered on magnets in the reduction plants.

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FILTRATION EFFICIENCIES OF BOOTHBAY DEPRESSOR TRAWLS

Boothbay Depressor Trawls (Figure 1) are used to obtain yearly estimates of the abundance of larval herring, *Clupea harengus harengus* Linnaeus, in the coastal water of the Gulf of Maine. The Boothbay Depressor trawl is a relatively new device (Graham and Vaughan, 1966), and its use is contemplated by others. It differs from other nets towed for collecting larval fishes in that a large depressor blade is located below the mouth opening and a liner is hung in a larger meshed net some distance from the mouth. These features of construction were examined to determine whether they affected the filtration of water through the trawls. Flow determinations were made about the depressor blade and trawl mouth, and the flow of water through the liner mouth was compared to the ambient flow.

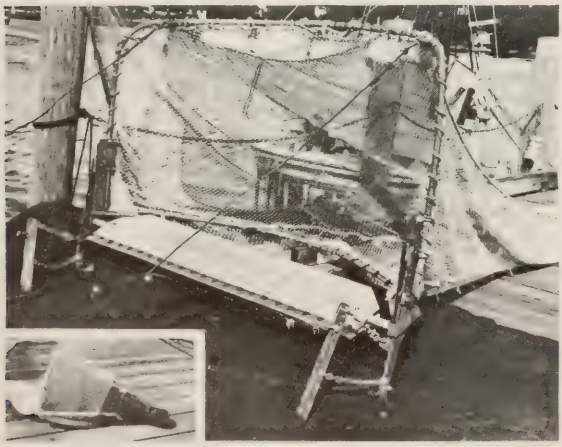

FIGURE 1.—Boothbay Depressor Trawl No. 1. Insert shows wire cod end.

Methods

Nets with a mesh opening of 3.2 cm stretched measure were lashed to pipe frames of 1 × 1.5 m, 1 × 2 m, 1.25 × 3 m, and 1.5 × 4 m (height × width), trawl No. 5, 1, 4, and 2, respectively. These large meshed exterior nets served to hang and protect the small-meshed liners (Table 1) of nylon webbing which retain the larvae. The diameter of the mouth opening for a liner was selected empirically. It was first hung throughout the length of its funnel-shaped exterior net. To reduce friction the liner was progressively shortened toward the cod end until the ratio of wire out to the depth sampled approached 3:1, during repeated tows at 4 to 6 knots. Construction details for the trawls and their respective nets are available from the author.

TABLE 1.—Descriptions of liners used with Boothbay Depressor Trawls.

Trawl type	Total length of liner	Mouth dimension of liner		Mesh diameter	Ratio of open areas
		Height	Width		Mesh/Mouth
	cm	*cm*	*cm*	*mm*	
No. 1	345	53	102	1	7.5
No. 1	579	89	113	2	7.7
No. 1	579	89	113	4	11.2
No. 2	700	152	274	2	5.3
No. 4	510	100	145	2	5.6
No. 5	510	100	145	2	5.6

The filtration efficiency of a No. 1 trawl containing a liner with a mesh opening of 4 mm was determined in a flume (circulating water channel) at the U.S. Navy's David Taylor Model Basin under experimental conditions as described by Mahnken and Jossi (1967). Velocities in the mouths of the pipe frame and the liner were measured by lowering a flow meter at intervals equivalent to its diameter and recording the velocity for each interval with a remote electronic counter. These velocities were then weighted by the area of each interval to obtain an average value for the entire mouth area. Also, a meter was fixed in the center of the forward opening of the wire cod end. Filtration efficiency was measured as the velocity recorded in the net divided by the velocity recorded in the flume; the quotient was expressed as a percentage. Dye was released within the mouths of the net and liner, and tabs were fixed to the blade and nets to trace the direction of the flow of water.

Several tests were made in the field to compare with the results from the flume. Field observations were carried out on (1) the same trawl used in the flume; (2) the trawl No. 2

having the lowest ratio of areas of mesh opening to mouth opening, and thus the lowest potential for efficient straining; and (3) the filtration of the liner mouth opening of trawl No. 5.

Eight flow meters were mounted within the pipe frame and one meter was mounted in the cod end of the same trawl and net (trawl No. 1) used in the flume. The eight meters were distributed peripherally and centrally within the mouth opening of the trawl to sample variations in straining by the net. Upstream and downstream tows were timed over a measured distance within a narrow estuarine channel and the results of the two tows were averaged to adjust for tidal currents. The experiment was repeated using a No. 2 trawl with a liner mesh opening of 2 mm, but flow meters could not be mounted within the liner mouths.

In constructing trawl No. 5, I made the dimensions of the depressor, of exterior net and liner equivalent to the mouth opening of the liner in trawl No. 4. Both the exterior net and the liner extended back from the trawl mouth. Six flow meters were dispersed within the mouth of the liner, one in the cod end, and two were mounted within a small frame outside of the net mouth. In this instance efficiency was considered to be the percentage of the average distance of the upstream and downstream tows recorded by flow meters inside and outside the liner.

I did not weight the velocities recorded in the field according to sectors of the mouth area metered in the net and liner as in the case of flume experiments. In the flume variations in flow were largely vertical, but in the estuary large lateral variations were known to occur. The number of flow meters necessary to make such integrations might have been sufficient to physically affect the flow through the net. A mean velocity recorded by the meters mounted within the mouths of the net and liner was used.

Results and Discussion

The No. 1 trawl was highly efficient at the flume velocities tested. The comparison of the velocities measured in the nets to the flume velocities (Table 2) gave an efficiency of approximately 100%. Efficiency in the cod end approximated 83%. The release of dye and the alignment of tabs showed that the flow of water could be traced horizontally through the net and the liner and that this flow was not diverted by the blade. Moving picture films of the trawl during the test are available from the author.

TABLE 2.—Flume and metered velocities for the Boothbay Depressor Trawl No. 1.

	Net mouth		Liner mouth			Cod end			
	cm/sec		*cm/sec*			*cm/sec*			
Metered velocity	205	309	156	238	314	156	238	309	314
Flume velocity	208	308	156	231	317	126	200	248	262

TABLE 3.—Vessel and metered velocities of the Boothbay Depressor Trawl No. 1 and 2.

	Net mouth	Cod end				
	cm/sec	*cm/sec*				
No. 1 trawl:						
Vessel velocity	184	200	203	192	184	198
Metered velocity	186	187	187	185	188	190
No. 2 trawl:						
Vessel velocity	207	207	222			
Metered velocity	196	157	175			

TABLE 4.—Metered distances of tow for Boothbay Depressor Trawl No. 5.

	Liner mouth		Cod end	
	m		*m*	
Outside	856	763	854	763
Inside	864	821	601	763

The results from field trials are similar to those obtained in the flume (Tables 3 and 4). Flow efficiencies at the net mouths of the pipe frame and at the liner mouth were comparable to those obtained in the flume. Efficiencies obtained in the cod end of the nets fluctuated around those (80-84%) from the flume. These results suggested that the depressor blade and the hanging of the liner within a larger net did not affect filtration efficiency. The efficiencies were independent of the velocity of towing and the ratio of the mesh to mouth openings, as would be expected with nets that were longer than twice the diameter of their mouth openings (Tranter and Heron, 1967). Further, it is unlikely that the efficiencies would decrease during sampling. Observations in the flume showed that the net and liner would be cleansed constantly during a tow by vigorous peristalsis of

their walls, similarly to that recorded for plankton nets of finer mesh (Tranter and Smith, 1968).

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SCIENTIFIC EDITOR'S NOTE

This issue of the *Fishery Bulletin* is dedicated to Dr. Oscar Elton Sette who, until his retirement, was a senior scientist of the National Marine Fisheries Service and its predecessors. All of the contributors owe a debt of gratitude to Dr. Sette and have used the following pages to express their appreciation to him. However, the number of contributors to this issue is only a small fraction of the fishery scientists who have been significantly affected by knowing this fine man. It is for all of them that I say thank you, Dr. Sette.

Reuben Lasker

Oscar Elton Sette.

OSCAR ELTON SETTE

I cannot imagine a more pleasant task than this—to write a prefatory statement for the Oscar Elton Sette issue of the *Fishery Bulletin*. It is also a most difficult task, for one must choose one's words with care lest he become maudlin and guilty of oversell on the one hand, or reserved to the point of disparagement on the other.

I do not propose to list Elton Sette's accomplishments and honors (these are recited elsewhere), but only to comment on and quote others on certain aspects of his career that may help us attain perspective.

It was not long ago that I left the 18th meeting of the Eastern Pacific Oceanic Conference (EPOC), before its conclusion and before Elton Sette stepped down as Chairman of that eminently successful "non-organization." He had conceived the idea and served as the sole (always temporary) Chairman through the history of this informal, nonstructured conference, at which attendees speak freely, representing only themselves in their capacity as experts and not necessarily speaking the party line of their parent organizations. The success of EPOC in developing ideas and plans, in bringing about coordinated efforts over a wide spectrum of scientific disciplines, is a measure of the way the man works: low key, low pressure, high performance.

Over a decade ago, on January 16, 1961, he received the Department of the Interior's highest honor, the Distinguished Service Award. In his citation, Secretary of the Interior Fred A. Seaton said this:

> Dr. Sette is an internationally recognized leader in marine science, highly respected by his contemporaries in University, State, and Federal Service. His ability has speeded progress in the knowledge of the sea and its resources, and reflected prestige and credit upon the Bureau of Commercial Fisheries and the Department. Since joining the Bureau of Fisheries, a predecessor agency of the Fish and Wildlife Service and Bureau of Commercial Fisheries, on January 8, 1924, he has made outstanding contributions not only as a scientist, but as an organizer of investigations, eminent administrator, and an unusually successful teacher . . .
>
> He has always placed special importance on the training of scientists under his supervision and has devoted much time and effort to their development. These efforts have had an important influence upon fishery science in the United States and Canada, as attested by the numbers of his former employees who now hold leading positions in the profession.

That such things should be said of a man who has already made a significant impact for the good upon society is appropriate and expected. But I find two earlier statements of perhaps greater interest for they show that his attributes were recognized at the very earliest stage of his career.

Some 50 years ago (fifty!), W. F. Thompson was Director of the fledgling California State Fisheries Laboratory. He employed a young college student, O. E. Sette, apparently in 1919, and wrote this for the January 1921 issue of "California Fish and Game":

> Mr. O. E. Sette, who has been with the [California] Commission for more than a year, has also returned to his college work, having left for Stanford on September 1 [1920] . . . . The Commission is fortunate in being able to retain the interest and services of Mr. Sette, whose work has been of high value.

Then, in January 1924:

> The fisheries investigation work of the Commission appears to be a training school for government fisheries men, for several who have been mainstays have been tempted to other positions by higher salaries . . . now comes word that O. E. Sette has accepted a prominent position with the United States Bureau of Fisheries . . . . Nor is it an easy matter to find the right kind of scientifically trained men to fill these vacated positions. Although discouraging, those in charge are planning to carry on by acquiring the best material available to fill these positions.

His worth was obviously apparent at a most tender age to no less stringent a taskmaster than W. F. Thompson.

From a personal standpoint, I knew him by repute from my first delvings into fisheries

literature as a student. My first real contact with his work came when, as a very junior biologist at that same State Fisheries Laboratory, I was given the task of recompiling some length frequencies of Pacific mackerel, which were measured in units called "settes." The man I knew of, the measurement not. It turned out he established the half centimeter as appropriate for mackerel during his days at the laboratory. The unit later became known as the sette, and the term was used for over a decade until the half centimeter finally fell from grace, being deemed insufficiently precise. I first met him some years after my encounter with the sette and found that the good reports that preceded him were excelled only by the man himself.

So with this issue we honor as best we can someone who has earned the respect and admiration of those fortunate enough to have crossed his path during his long and most honorable career. He is in the truest sense a gentle man.

Philip M. Roedel

OSCAR ELTON SETTE: FISHERY BIOLOGIST

PATRICIA POWELL[1]

The twentieth century marked a turning point in the development and advancement of many scientific disciplines. Pioneer leaders at this time turned to research, focusing their explorations on ways and means of increasing man's knowledge about himself and of the world in which he lives. Within a lifetime, these leaders made an impact on society that changed social and economic structures and continues to do so. Oscar Elton Sette, fishery biologist, is one of this select group. His contributions to marine fisheries and his astute administration of fishery research places him among the foremost of his contemporaries. He pioneered research in two oceans. He was among the first to expand the concept of fishery biology to include other disciplines, and succeeded in integrating this science with those of oceanography and meteorology, elevating it to a major status and advancing its economic importance worldwide.

A midwesterner by birth, Sette spent his early years in an environment quite different from that which was to hold his attention for more than fifty years. His parents, Martin and Louise, lived in Clyman, Wisconsin, where his father owned a retail lumber business. On March 29, 1900, their fourth child Oscar Elton Sette was born. The Settes also had two daughters and another son. A few years after Elton's birth, the family moved to a small town of Juneau, Wisconsin, for business reasons.

It was in Juneau that Elton, as he preferred to be called, learned reading, writing, and arithmatic; and developed a lasting love of nature, together with a scientific curiosity concerning all living things. He says his great love was for "natural history studies," particularly those of butterflies. At a very early age, he collected butterflies which he classified, and had a truly remarkable collection of Lepidoptera by the time he finished high school. He has continued to collect these insects throughout his life, and when work pressures were great in later years, claims this hobby afforded the release he needed to prevent ulcers. He also collected stamps.

Martin Sette always wanted to retire on a lemon ranch, and with this in mind bought five acres near Chula Vista, California. Later he bought another five acres. When some of his investments went "sour," he decided to live on the ranch and grow lemons. The family moved to southern California in 1910. During some lean years that followed, Elton's mother, who firmly believed in the principle of "waste not, want not," instilled a sense of frugality in her children. This quality, which Mr. Webster defines as "careful management of resources," has been reflected in her son's thinking down the years.

Between the ages ten and sixteen, Elton was kept busy with school activities and the pursuit of his hobbies. He graduated from the eighth grade when he was twelve, then attended high school in National City, California, for four years. He was an outstanding student and planned to enter college, expecting to get a degree from the University of California at Berkeley in Entomology. However, fate, by the name of Elmer Higgins, stepped into the picture in 1916. Owing to a chain of circumstances in which Dr. Higgins played a part, Elton's plans for college did not materialize. Instead of becoming a "bug-hunter," his interest was diverted from butterflies to fisheries. His first encounter with this gentleman came during his senior year in high school. The following is a quote from an anectodal review of Elton Sette's career as written by Elmer Higgins:

> "My first contact with Elton Sette occurred in September, 1916, when a trim, compact, boy in knickers and shirt filed into my chemistry classroom and laboratory with a couple dozen other students in National City (Calif.) High School. I was a 'freshman' science

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teacher on my first job after receiving my secondary school teacher's certificate and in my zeal I must have borne down rather heavily on my students, but most of them took it and seemed to like it.

"Came the end of the first 'advisory period' and I reported three or four students to the Principal as failing to make satisfactory grades. Among them was Elton Sette. The next day, the Principal came to me with a worried expression to ask what was the trouble, explaining that Elton was starting his senior year and everyone expected him to graduate with honors. I agreed that Elton was learning chemistry (witness the very good grades he earned in the frequent little written quizzes), but he seldom was prepared to recite on the day's assigned section in the textbook and, moreover, his laboratory notebook was quite incomplete.

"Elton apparently had acquired the habit of listening intently in class to the recitations and discussions of his more diligent classmates, sorting and storing the pertinent facts in his retentive and discerning mind, and instantly recalling them to write an excellent examination paper. The Principal gravely agreed to speak to Elton. Elton's performance immediately improved, and he went on to graduate as the Valedictorian of his class."

Almost two years passed before Sette encountered Elmer Higgins again. He had been attending San Diego Junior College, with definite plans to enter the University of California in the fall of 1918. Then, one day as he was walking down a street in San Diego, they happened to meet. Higgins invited Elton to accompany him on an exploratory trawling trip. When Elton saw what came up in the nets, he was fascinated. He knew right then he wanted to become a fishery biologist. Elmer Higgins was now working at the California State Fisheries Laboratory in San Pedro as a scientific assistant. Dr. Wm. F. Thompson, Director of the Laboratory and in charge of fishery investigations in southern California, was especially interested in the albacore fishery, and needed observations of landings from San Diego. He asked Higgins if he knew of any former student who could be recruited for summer work. Higgins immediately wrote Sette who agreed to check the canneries for albacore landings. So, Elton Sette, through the chance intervention of Elmer Higgins, began his career working with fisheries at 18.

He did not enroll at the University in Berkeley that fall as planned. Instead, he joined other young men his age and served in the U.S. Army. World War I was in the final stages. Upon his discharge in 1919, he joined the staff of the State Fisheries Laboratory.

A definite program of scientific investigation concerning the sardine was inaugurated in 1920 by Dr. Thompson. The increasing commercial importance of this fishery made it necessary to learn about sardine habits and determine the effects of fishing on the resource. Elton Sette was assigned to this investigation from the beginning. He was sent to Monterey, the center of the great sardine canning industry.

In his first report, Sette wrote "Hopkins Marine Station courteously granted the Fish and Game Commission use of quarters and facilities." Other accounts described his office as "a daydreamer's paradise, punctuated with bird watching, and girl watching, in the picturesque cove below." In spite of distractions, he states the investigation was carried on "energetically." His first article was published in *California Fish and Game* in October 1920. In this publication he described the Monterey fishery, his work, and expressed a prophetic interest in the yearly fluctuations in abundance and sizes of the fish as well as concern for the fishery unless "intelligent conservation measures" were adopted. This early interest in the underlying causes of fluctuations in pelagic fish abundance and what can be done to prevent the depletion of these resources has remained with him throughout the years.

In September 1920, he took a leave of absence to attend Stanford University to finish college. His two years there were rich ones, for under David Starr Jordan's guidance Stanford was the center of fisheries research on the west coast. Many Stanford graduates became outstanding leaders in various aspects of fishery science. It was a great peer group, and lifelong associations were formed in the inspiring, informal gatherings where ichthyology and research problems were discussed. But it was not all work or talk. Sette found time to play tennis and collect butterflies on Jasper Ridge. He graduated with a Bachelor of Arts in Zoology in June 1922.

After graduation Sette continued his work with the State Fisheries Laboratory, as a scien-

tific assistant, alternating between Monterey during the sardine fishing season and the San Pedro Laboratory to work on tuna investigations in other months. His first major contribution to fishery literature reported his analysis of the sardine data he collected at Monterey as well as various sampling systems he used. It was submitted for publication in April 1924.

Sette used an increasing amount of statistical analysis in his study of the sardine fishery. This came to the attention of U.S. Commissioner of Fisheries, Henry O'Malley, who persuaded him to move to Washington, D.C. and join the U.S. Bureau of Fisheries as Chief of the Division of Fishery Industries. He held this position from 1924 to 1928. Managing this division included supervising research in fishery technology, particularly the canning and preservation of fishery products, and the distribution of technological and production information to the public. He also was given the special task of improving the Federal Government's system of collecting and publishing statistics. During this time, his own publications were confined to annual statistical and economic reports of United States fisheries, and articles concerning commercial fisheries for Bureau publications or trade journals.

The year 1924 was one of change and growth for Elton. Living in the capital city was quite different from that of the west coast, the new job was entirely different from that of his previous experience, and he relinquished his bachelorhood. He had met and fallen in love with Elizabeth G. Jackson whom he married December 20 of that year.

The new job was stimulating, but Sette never lost his interest in fishery biology, nor in the challenge to manage large fluctuating fish resources. So he began on his own to study the Atlantic mackerel which had yielded widely different catches over a period of years. Once again Elmer Higgins entered his life. Higgins had been appointed Chief of the Division of Scientific Inquiry, U.S. Bureau of Fisheries, and was stationed in Washington, D.C. He encouraged Elton in his mackerel research and offered him a position in his Division as full-time investigator. Sette decided to accept in 1928. Meanwhile, increased appropriations from Congress made it possible to establish regional research teams to investigate important fisheries, or types of fisheries. Because of his experience and personal competence, Sette was made Chief of the North Atlantic Fishery Investigations, a position he held until 1937.

He established headquarters at the Museum of Comparative Zoology at Harvard University, and recruited a handpicked staff to study the life histories of marine fish important to the New England coast as well as the effect of fishing on their abundance. At the same time, Sette concentrated his own attention on the Atlantic mackerel. The published results of this study represent a significant contribution to fisheries research and is a classic in the literature. During the summer months he acted as Director of the Bureau's Fisheries Station at Woods Hole. He also found time to continue his studies, at the graduate level, and obtained his Master's Degree in Biology at Harvard in 1930. Of Sette and his staff, Dr. Higgins wrote:

> "..... (they) worked in a sort of happy symbiosis with the staff of the M.C.Z., the Faculty, and graduate students, many of whom were employed by the Bureau on temporary appointments. Thus, the haddock investigations began, the cod investigations wound up, the weakfish studies of the mid-Atlantic coast were extended, and oceanographic examination of the Gulf of Maine was brought to a virtual completion. All of these efforts resulted in a number of significant papers."

One of Sette's most endearing qualities to those who worked under him, especially students and young men starting their careers in marine science, was his ability to meet with them and discuss work at their level, to draw them out, and inspire them to put forth their best effort. One such student was Dr. Daniel Merriman, present Director of Sears Foundation for Marine Research. He worked part time for Sette in the summer of 1930 while he was taking an invertebrate course at the Marine Biological Laboratory. He has written:

> "I cannot imagine how I got the job unless it was through the good offices of Dr. Henry Bigelow, a close family friend. My record at Harvard had nothing

to commend me, and the only thing I can think of was a teen-age association with Dr. A. G. Huntsman at St. Andrews, New Brunswick. In all events, I sorted mackerel eggs and larvae to a fare-thee-well. But the point is, the work never became tedious under Sette's watchful eye. I thoroughly enjoyed it and him, and in vicarious fashion I learned a lot; it was by far my most rewarding summer to date. Bigelow, Huntsman and Sette: three men who nudged an aimless youngster into a happy and rewarding career. I shall always be eternally grateful to O. E. S. for his patience and his stimulus."

Forty years later another young man, just starting his career, has written:

"During the summer of 1965 I worked in Dr. Sette's Lab as a seasonal aid type. I learned more in 2½ months working with Dr. Sette and his staff than I did in the 4 years at the College of Fisheries. The people who work with Dr. Sette work as a team. Each individual has his own talents and Dr. Sette augments these talents. Somehow through empathy and compassion he frees you to your limitations and helps you to work beyond your own ability. Each specialist from secretary to oceanographer is fully aware of the entire effort.—there are far too few Dr. Settes."

So wrote Richard A. Winnor, Associate Marine Biologist, California Department of Fish and Game, in 1972.

Sette's pleasant days at Harvard and Woods Hole lasted nine years, in which time knowledge of fishery resources on the Atlantic coast was advanced significantly. Meanwhile a crisis was developing on the Pacific coast. The sardine fishery, which gave indications of mushrooming back in the early twenties, had expanded beyond all expectations within two decades. From 1916 through 1939, the catch more than doubled each six years, and reached its maximum in 1936 with a billion and a half pounds landed. State fishery biologists were concerned and warned against overfishing. Nationally, concern for the nation's food supply was developing, and demands were being made for a better scientific basis of fishery management. Since the state was unable to control the fishing industry through legislation, a Congressional investigation was made. Because of his proven ability to manage a fishery resource, his past experiences with the sardine fishery, and his contacts with the industry, Sette was sent to California by Congressional mandate, to head a sardine research program inaugurated by the Bureau, a position of great responsibility. He was made Chief of the new South Pacific Fisheries Investigations, with headquarters on the Stanford campus. His duty statement proclaimed "he was to direct and perform research on the nature and causes of fluctuations in pelagic fish populations." This fooled no one. N. B. Scofield, Chief of the State Bureau of Marine Fisheries, resented federal intervention in California fisheries investigations and openly remarked the best thing Sette could do was to pack his bags and go back to Washington. The industry also wanted no federal intervention and regarded Sette's operations with suspicion. However, his mild and friendly personality had won him many friends among the industry in the early twenties. Those who did not know him had a great respect for his work and his personal honesty, as did the biologists with the Division of Fish and Game, many of whom were old friends. His marked success in handling this delicate situation is an example of Sette's personal tact and diplomacy.

For several years strong disagreements existed between the industry and the Fish and Game Commission. Canners were critical of techniques used by the State's biologists and of

John L. Hart, Fisheries Research Board of Canada, and O. E. Sette.

their evaluation of the sardine data. As a result, the San Francisco Sardine Association and the California Sardine Products Institute engaged Sette as a paid consultant from 1942-1947. Their respect for his judgement was so great they followed his advice without question when he said he could not conscientiously recommend industry requests for additional tonnage. Julian Burnette, a prominent business man who was active in industry affairs during that time, commented that Sette never spoke unless he had something to say, and when he did, people listened.

Marine fishery research was practically eliminated during World War II owing to a manpower shortage and the use of fishing vessels for the war effort. Between 1943 and 1945, Sette served as Area Coordinator of Fisheries for California. He applied strict control on all plants and vessels that were operating in the California fisheries. He assigned boats to different plants and shifted them around so all plants would be in operation and no waste would occur. Controlling a fiercely competitive industry was an especially difficult assignment. His success was rewarded by a meritorious promotion in 1944, in his capacity as Chief of the South Pacific Fisheries Investigations where he remained until 1949.

The post-war years witnessed a boom in commercial fishing and ushered in a period of expansion in fishery research. The search for new sources of protein to meet the demands of a growing population, as well as the economic aspects of harvesting large pelagic fish stocks attracted monied interests internationally. The need to discuss mutual problems and exchange information between scientists engaged in fishery research in other countries resulted in a series of international meetings. Sette attended several of these as an official representative for the United States.

Meanwhile the sardine fishery in California experienced an alarming decline. Concern over the depletion of this resource gave rise to public demand for answers from fishery biologists to explain what caused the fluctuation of this once great fishery. The answer to this problem already had challenged Sette's thinking for a quarter of a century. It was obvious that such answers could be sought only through the cooperation of various agencies working together on a multidisciplined research program. In 1947 the California State Legislature established the industry-financed Marine Research Committee. The Committee, consisting largely of industry members, and with Sette as its scientific advisor, inaugurated the California Cooperative Sardine Research Program which became the California Cooperative Oceanic Fisheries Investigations, or CalCOFI. Five agencies participated at the Federal, State, and University levels. Sette's fine hand was evident throughout the planning stages. He was largely instrumental in integrating the disciplines of fishery biology with those of oceanography and meteorology as this program developed. His personal contributions to the program and his participation in symposia at annual meetings were significant.

The fishing pressure exerted on tuna stocks throughout the Pacific ocean prompted the federal government to initiate tuna research in the mid-Pacific in 1949. Money was appropriated to build a large, well equipped laboratory adjacent to the University of Hawaii campus and to purchase two vessels designed for this specific program. Sette was appointed Director of the new Honolulu Laboratory and made Chief of the Pacific Oceanic Fishery Investigations, or POFI as it was called. Here, under his leadership, an exceptional research staff was assembled. The team, consisting of fisheries biologists, oceanographers, and meteorologists, jointly launched another pioneer program to study environmental phenomena and their relationship to oceanic fishes. In their studies of tuna resources along the equator, a subsurface current was detected. The name of this current honors its discoverer, Townsend Cromwell. The masses of other data published provided a great source of new information about the central Pacific Ocean.

While in Hawaii, Sette was an enthusiastic gardener and he took great pride in his flowers, fruits, and vegetables. He recycled matter for his own compost long before recycling became a popular conservation measure. His zeal for composting caused a family crisis. Apparently his wife, Elizabeth, thought the compost was

Staff of Pacific Oceanic Fishery Investigations, Honolulu, Hawaii. Left to right: Walter M. Bosworth, Administrative Assistant; Keith Elliott, Statistician; Harold T. Smither, Administrative Officer; Donald L. McKernan, Assistant Director; O. E. Sette, Director; Harry B. Hinkle, Operations Officer; Albert K. Akana, Marine Operations Superintendent.

(Photograph courtesy of *National Fisherman*)

responsible for breeding centipedes, which reach considerable size in Hawaii. Often they found their way into the house where Mrs. Sette received several bites. These she was quick to blame on her husband and his compost.

He was also an avid tennis player, and a good one. While at POFI he encouraged and organized tennis tournaments at the Lab. When a tournament was held, it was mandatory that a player show up for the matches, no matter how severe the hangover.

Representatives of the tuna industry did not think Hawaii was the right location for the Bureau's tuna investigations. They wanted this research centered in California near the tuna canneries and the fishing fleet. Charles Carry, Director of the Tuna Research Foundation and spokesman for the industry, often gave Sette a bad time about this and other matters. In this connection, Carry tells about an incident that happened in Santiago, Chile, where he and Sette were attending an international fisheries meeting in 1955. In all of Carry's frequent trips to the Honolulu laboratory, he had never seen Elton take a drink, and knew it was because he suffered from stomach ulcers. But in Santiago, Elton drank with the rest of the group. Carry asked why. Sette replied, "I have learned not to take myself too seriously, nor you, Charlie."

Each new assignment in Sette's life was an expansion of his original interest. For five years at POFI, his primary responsibilities were to direct research and exploration on potential fishery resources. Then in 1955, a new program called Ocean Research came off the Bureau's drawing board, and once more Sette was called to pioneer a new direction in fishery research. He was returned to the Stanford campus as Chief of Ocean Research and director of another new laboratory broadly chartered to examine all available data concerning the oceans and relate these to the abundance and distribution of fish. He set about the herculean task of analyzing masses of sea surface temperature data, weather observations, and all known information concerning fish availability. With the help of a small but highly skilled team of biologists, oceanographers, and meteorologists, an atlas containing 168 monthly mean sea surface temperature charts for the Pacific Ocean north of latitude 20°, covering the years 1949-1962, was published. This remarkable man still found time to complete

his graduate work, receiving his Doctorate in Biology from Stanford University in 1957; to give lectures at the University; to continue collecting butterflies on Jasper Ridge as he had done in his student days; and to publish on a species of Lepidoptera from central California.

Sette always has been a firm believer in the value of informal meetings. He was instrumental in organizing the Pacific Tuna Conferences; he helped structure and actively participated in the CalCOFI Conferences as he had in the Sardine Meetings from their beginning in 1920. He chaired, or was a committee member of, numerous planning and steering committees throughout the years. EPOC was a natural outgrowth of his experience working with groups.

In 1954 at a meeting of the Oceanography Fisheries Meteorology Committee, Sette proposed that various groups engaged in related investigations in the eastern Pacific join together to coordinate the planning and execution of work at sea, and to exchange information on research program results. His proposal was acted upon in the Committee's 1955 meeting, and EPOC, or the Eastern Pacific Oceanic Conference, was born. EPOC held its first meeting in 1956 with Elton Sette as chairman and Joseph L. Reid, Jr., as Secretary. For fifteen dedicated years both men served EPOC and the entire ocean science community. They made possible a forum for discussion of oceanographic research and provided a medium by which the farflung investigations of diverse academic and governmental agencies could be coordinated.

Dr. Sette's administration of international oceanographic investigations to study stocks of fishes that recognize no political boundaries, brought him in close contact with scientists of other countries who also were interested in these pelagic resources. He attended many international meetings to discuss common problems. He was an official United States delegate to the Indo-Pacific Fisheries Council in Singapore in 1949 and to the International Technical Conference on the Living Resources of the Sea in Rome in 1955. He acted as Advisor to the U.S. Delegation at a Fisheries Conference, Santiago, Chile, in 1955, and at the Law of the Sea Conference, Geneva, 1958. He participated in numerous other meetings as a committee member, council correspondent, or by presenting a paper.

He has served as a consultant on oceanography to the Director of the Bureau of Commercial Fisheries and as special consultant to the Atomic Energy Commission. He was a member of the Ocean Resources Panel of the National Academy of Sciences and is an advisor to the University of California, Institute of Marine Sciences.

Numerous professional and technical societies have his support as an active member, including Phi Beta Kappa and Sigma Xi. He is a founding member of the American Institute of Fishery Research Biologists, and a Fellow of the American Association for the Advancement of Science. Others include: American Fisheries Society; American Institute of Biological Sciences; American Society of Ichthyologists and Herpetologists; American Society of Limnology and Oceanography; American Wildlife Society; Biometric Society; California Academy of Sciences; Oceanographic Society of the Pacific; and, Western Society of Naturalists.

For outstanding service to the Federal Government, Oscar E. Sette was presented the U.S. Department of Interior's gold medal award for distinguished service on January 16, 1961. The medal and citation delivered by Assistant Secretary Leffler before an audience of several hundred reads in part as follows:

> ". . . . In recognition of his important contributions to the scientific program of the Bureau of Commercial Fisheries and his eminent career in Government, the Department of the Interior bestows upon Dr. Sette its highest honor, the Distinguished Service Award.
>
> FRED A. SEATON
> Secretary of the Interior."

It seems more than coincidental that sitting on the stage beside Dr. Sette that day was Dr. Elmer Higgins, who also received the Distinguished Service Award for outstanding achievement.

Dr. Sette's accomplishments are legion. It would be difficult to select any one as the most outstanding. He modestly sums up what he considers to be his major achievements in two succinct statements. These are: contributions to knowledge regarding pelagic sea fish and fisheries; and, the planning, organization, and

Opening a cocoanut, Hawaii.

directing through their formative years, the four research programs he administered for forty-two years. Equally significant, and perhaps greater, is the sustaining influence he exerted throughout the years as Chairman of EPOC and a guiding member of CalCOFI and other such research groups. Here, his uncanny ability to foresee a problem situation and sidestep the issue before it became a crisis was especially valuable. Also important are the untold hours of service rendered government agencies, the scientific community, the industry, and others as a technical advisor, special consultant, official delegate, leader, and friend. Over and above all is the remarkable contribution of the man himself through his personal warmth, his unusual ability to inspire, his patience and perception as a teacher, his gift of enthusiasm for his own work and that of others, and most of all, his genuine interest in and love of people.

There is an impressive list of publications to Sette's credit, in spite of his time-consuming administrative responsibilities. Several have been mentioned above. Other important papers include: *Estimation of the abundance of the eggs and larvae of the Pacific pilchard off southern California during 1940 and 1941* (Sette and Ahlstrom, 1948); *Considerations of midocean fish production as related to oceanic circulatory systems* (1955); *Problems in fish population fluctuations* (1961); *Ocean environment and fish distribution and abundance* (1966); and *A perspective of a multi-species fishery* (1969).

Sette also found the time to keep up with current literature in his own fields as well as that of others which intrigued his scholarly or scientific interests. His own library is extensive, and he, personally, has indexed most of the material pertaining to ocean sciences. Sette's memory is retentive, and when asked, he can call to mind papers on specific subjects, although the article may have been written years ago.

When asked his choice of a place to live, he chose California, with its long coastline and mild sunny climate. He and Mrs. Sette make their home in Los Altos where they have resided for many years. They are a devoted family, and enjoy having their only daughter, Josephine Helene Barnes, and her family live nearby in San Jose. The Robert F. Barnes have two young sons, ages four and seven, who are a source of great pleasure to their grandparents.

Needless to say, the Settes' garden is a place of beauty, as well as a practical source of food. Planned with the precision of a research program, the yard is planted in rotation to produce a continuous supply of fresh vegetables and flowers from early spring throughout the fall months; and, they enjoy a succession of fruit in season from the many varieties he has cultivated or skillfully grafted to parent trees. The flowers attract the butterflies Sette loves, and have given rise to a backyard investigation, in his spare time, of a subtropical species *Agraulis vanillae*, which appeared early in 1960, enticed by the passion flower plants growing in the garden. Hoping to keep the small population alive during the winter months, Sette started growing passion flowers in the lathe house to protect the eggs and larvae from unaccustomed cold. He began to study the fluctuation of their populations, observing the time of emergence and the relationship to warmth and sunshine. This correlation to warm, sunny spring days fostered an interest in amateur meteorology, which has developed into another hobby. Daily he observes the humidity and the barometric pressures and follows the passing lows and highs with interest. This keen sense of awareness of his surroundings is a delightful part of his personality.

On paper, in compliance with government regulations, Dr. Oscar Elton Sette, Senior Scientist, "retired" in March 1970. He was immediately rehired as an "annuitant" which is permissible in Federal service, to continue his research and prepare for publication a backlog of data. The Ocean Research program was concluded in June 1970, and the laboratory at Stanford was closed. He is presently attached to the Tiburon Laboratory, National Marine Fisheries Service, in charge of the Ocean Ecology unit, headquartered in Menlo Park. With the assistance of a secretary-librarian his keen mind is busily engaged with many of the unsolved problems facing fishery researchers. He is working on several papers, one of which is the analysis of the Alaska herring fishery. His duty statement on his appointment papers fill two typed pages, single spaced. They end with ..... "a high degree of confidence is placed on his productivity, competence, and judgement. He is recognized as a top authority and distinguished scientist in his field." It is interesting to note that his present title is: Fishery Biologist (Research).

For more than half a century Dr. Oscar Elton Sette, fishery biologist, leader of leaders, has continued to pioneer the development and advancement of fishery research as an outstanding scientist, a great humanitarian, and a warm and sincere friend to all of his associates.

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RESEARCH AND THE FISHERIES SERVICE'S SECOND 100 YEARS

PHILIP M. ROEDEL[1]

A year ago, in 1971, we celebrated the one hundredth year of a Federal fishery service. This was an occasion, depending upon the individual, for self-congratulation, a tabulation of a century of successes, wonderment that so many could accomplish so little in so long, and on the part of a number of us serious thought and study of where the first century had brought us and whence we might wish the second to lead us. What can we learn from the past; how should we change our ways if we are to cope adequately with problems as we see them today and foresee they will be tomorrow?

The first century had its moments of great success, its moments of failure, and we can expect the same in our second, hoping and planning that there will be more of the former and fewer of the latter. This first century began with the era of descriptive ichthyology, with fisheries science as we know it today growing from these beginnings. We can follow the development of the science from one essentially zoological—and a limited range of zoology at that—to one encompassing all aspects of biology, particularly physiology and genetics, and going beyond the biological sciences to oceanography, mathematics, and statistical analysis in our attempts to understand and predict fluctuations in abundance. Rather late in the first century we find food science entering as a partner in fisheries research. Only recently has there been an acceptance, unfortunately still given grudgingly in some circles, of economic, social, and legal research as legitimate fisheries tools.

The first century, until its last decade or two, was one in which the pace was leisurely. There was time for thoroughgoing analysis, for programs that satisfied the scientist's legitimate and proper desire to have a full understanding of the system he was studying before making pronouncements on or recommendations concerning its status or management.

To be sure, it was concern over the status of certain stocks that led to the establishment of the Federal fishery service in 1871, and of, for example, the California State Fisheries Laboratory in 1917, and the International Fisheries (now Halibut) Commission in 1924. The collapse of the Pacific sardine fishery in the 1940's gave warning that the pace of research might be too slow, that scientists might be called upon for recommendations based on—to them—insufficient evidence, that fisheries science could ill-afford internecine warfare, and that a new breed of man, the skilled biopolitician, was desperately needed if the findings of the scientists were to be translated into effective laws in time to do any good for an overfished stock.

It was also forced upon our attention in the remaining two decades of this first century that other nations had indeed developed a new breed of fishermen, one that has changed all the rules of the game.

The tremendous fishing power of the distant-water fleets, their worldwide mobility, and their capability for pulse fishing finally brought home to us toward the close of the first century the fact that fisheries now could be explored, developed, exploited, overexploited, and left to their fate in far less time than traditional methods of stock assessment could give an estimate of optimal yield. We found also that existing political and institutional arrangements were not capable of responding to these new pressures.

To cope with this we must turn to rapid assessment techniques, reliance on data that once would have seemed pitifully inadequate, to "quick

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and dirty" surveys that are an anathema to the purist but vital in what we see as the real world today.

This last decade—the 1960's—has also brought forth most clearly that resolution of environmental problems is critical if we are to have any fish left for us—or other nations—to fish or if we are to pursue aquaculture as a significant means of food production. This area of research, tackling as it does matters of environmental quality, of the impact of environmental degradation on living organisms and in turn on man the consumer, and of what can be done about it, must be one of primary concern to us as we move into the second century.

Another set of factors is influencing our course of action most strongly. Fishery scientists and administrators, particularly the latter, have always been cognizant of them but have not as a general rule faced up to them. These factors deal with the common property nature of fishery resources and the economic and legal problems associated therewith. Quite obviously, the finest biological research in the world is of little avail if proposals for utilization or management based on its results cannot be implemented. On the one hand, we have serious problems of allocation of available stocks among political and social entities; on the other we have a series of regulatory systems that tends generally to perpetuate economic inefficiencies and to lead to overcapitalization.

The biologist cannot cope properly with these serious and highly complex problems, though too often he was forced to try in recent decades because the fisheries field simply did not have sufficient professional talent in such areas as law and economics associated with it.

The need for economic research has for some years been recognized as essential, and work in this area is going on apace in both the Federal fisheries service and in several universities. Economics is not, however, the only "new" discipline involved in the fisheries problems we now face. Legal research, particularly in the field of international and constitutional law, is obviously pertinent. It is equally critical as we become more and more concerned with domestic allocation and control of fisheries and the allocation of resources among competing users of the environment. Are estuaries for fish, for industry, for marinas—or for all of them, perhaps plus something else? Is a given species for the sportsman, for the commercial fisherman—or for both of them, perhaps plus someone else? Here we move into a generally unplowed field and that falls partly at least within the purview of still another professional—the sociologist.

In Century I, fisheries science moved from ichthyology into fisheries biology, added other biological disciplines such as physiology and genetics, accepted mathematics and statistics as integral to success, incorporated physical oceanography, engineering, and physics into the fold, touched on meteorology, became deeply involved with biochemistry and food science, and opened the door to economists and lawyers. The future will hold a greater role for the social sciences and the legal profession, but it will remain the fisheries scientist (whatever he may be—some mix of biologist, ecologist, oceanographer, and mathematician) who will provide the requisite scientific data with which other disciplines can interact to provide the final synthesis upon which the administrator can base his decision.

Research in the Fisheries Service at present falls into three major categories: (i) biological, ecological, and oceanographic research of the sort traditionally conducted by fisheries biologists, including fisheries oceanography, population dynamics, inshore ecology, studies of contaminants and disease, aquaculture, a smattering of gear technology and instrumentation, and so on; (ii) fishery technology and marketing research; and (iii) economic research, this of necessity growing to encompass matters of a social, institutional, or legal nature.

All of this is being carried on so that we may fulfill our mission as we see it: to promote the wise use of living marine resources for their aesthetic, economic, and recreational value to the American people. Our basic objectives within the framework of that mission are to understand and protect living marine resources and the environmental quality essential for their existence, and to devise rational schemes for resource allocation and development.

We are thus striving for many things in our research program. If they are to be of maximum value, they must produce results that will assist us in our attempts to keep as many fishery management options open to the Nation as possible.

We need, then, reasonably precise measures of abundance of the living marine resources, and of their response to varying types and degrees of fishing pressure—foreign, domestic, sport, and commercial. We need to know of their distribution in time and space, of the impact on them of environmental changes whether induced by man or by nature. We must cope with a wide variety of technological problems, some of them requiring short-term responses. And economic, social, and legal research must concern itself with a wide variety of programs, ranging from rather basic economic analyses of each fishery, to developing means for overcoming such problems as property rights and split jurisdiction, and determining the economic and social benefits of fisheries resources to the Nation.

It is within this framework and toward resolution of these problems that our programs and efforts are being redirected as the Fisheries Service enters its second hundred years.

DEVELOPMENT OF THE LANTERNFISH, *SCOPELOPSIS MULTIPUNCTATUS* BRAUER 1906, WITH A DISCUSSION OF ITS PHYLOGENETIC POSITION IN THE FAMILY MYCTOPHIDAE AND ITS ROLE IN A PROPOSED MECHANISM FOR THE EVOLUTION OF PHOTOPHORE PATTERNS IN LANTERNFISHES

H. Geoffrey Moser and Elbert H. Ahlstrom[1]

ABSTRACT

The larval and transformation stages of the unusual myctophid, *Scopelopsis multipunctatus* Brauer, are described. A character that the larvae of *Scopelopsis* share with a number of other genera in the Lampanyctinae is the sequential development of three or more pairs of early forming photophores. The sequence of development of early forming photophores is shown to be an especially useful character in revealing phylogenetic affinities when used in conjunction with other larval characters, such as body shape and pigment pattern. From our study of the development of *Scopelopsis*, a possible mechanism for the evolution of photophore patterns within the family Myctophidae is presented.

Brauer (1906), in his elegant report on the fishes collected during the German Deep-Sea Expedition of 1898-99, described for the first time a remarkable lanternfish, for which he established the genus *Scopelopsis*. His single specimen, a newly transformed juvenile, was unique in having the head and body studded with minute light organs, all of approximately the same size. All other lanternfish known to him were characterized by a specific pattern of photophores on the head and on the ventral and lateral regions of the body. These he grouped into the single genus *Myctophum*, under which he recognized four subgenera: *Myctophum, Diaphus, Lampanyctus*, and *Lampadena*. These two genera, along with *Neoscopelus*, a genus with an undifferentiated pattern of ventral photophores, and five other genera were included in the family Scopelidae.

Regan (1911) modified drastically this taxonomic arrangement by distributing Brauer's eight genera of scopelids into a scheme of three suborders. He placed the family Myctophidae within one of these suborders and included within it seven genera: *Scopelopsis, Neoscopelus, Scopelengys* (a genus related to *Neoscopelus* but lacking photophores), and the four subgenera of Brauer raised to generic rank. Parr (1928) further differentiated the family Myctophidae to include three subfamilies: Scopelengini for *Scopelengys*, Neoscopelini for *Neoscopelus*, and *Scopelopsis*, and Myctophini for *Myctophum, Lampanyctus, Diaphus*, and *Lampadena*.

Tåning (1932) noted that in a number of well-preserved specimens of *Scopelopsis*, certain photophores were larger and better developed than others, and that the scales covering these organs were equipped with the same lens-like modification typical of other members of Parr's Myctophini. He observed further that these larger photophores formed a pattern that corresponded with the kinds of photophore patterns found in the Myctophini and concluded, accordingly, that *Scopelopsis* belonged with *Myctophum, Lampanyctus*, and relatives in the subfamily Myctophini.

Fraser-Brunner (1949) reduced the number of subfamilies in the Myctophidae to two: The Neoscopelinae, to include *Neoscopelus, Scopelengys*, and *Solivomer*, and the Myctophinae, to in-

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clude *Scopelopsis* and 20 other genera. He provided the first substantial description of the photophore pattern of *Scopelopsis* and, in his illustration, differentiated the more conspicuous "primary" photophores from the minute "secondary" organs. Further, he recognized two major evolutionary lineages among these 21 genera and placed *Scopelopsis* among the group which included *Lampanyctus* and its relatives.

Authors since Smith (1949) have afforded full family status to the neoscopelines, separating the three genera from the Myctophidae. Recently, Paxton (1968) reviewed the osteology of the Myctophidae and constructed a higher classification to reflect generic relationships within the family. His views have been stimulative and complementary to our studies of larval myctophids (Moser and Ahlstrom, 1970). Our recent discovery of the larvae of *Scopelopsis* has served to crystallize our views of relationships within that part of the family which contains *Lampanyctus* and its allies. These ideas, based chiefly on larval morphology and sequence of photophore development, are set forth herein, following the description of *Scopelopsis* larvae.

MATERIALS AND METHODS

The developmental series of *Scopelopsis* used in this study was obtained chiefly from the R.R.S. *Discovery* plankton collections, housed at the British Museum (Natural History). A total of 29 specimens was taken off South Africa at stations 412, 413, 416, 418, 419, and 438 in August-September 1930. An additional five larvae were found on station 2352, occupied off South Africa in July 1938. A single transforming specimen came from station 2280 of the U.S. Antarctic Project ship *Eltanin*. Although adult specimens of *Scopelopsis* were obtained on EASTROPAC surveys, larvae were not taken.

A series of 25 specimens, from smallest larva to juveniles, was measured according to the method described in Moser and Ahlstrom (1970), to produce the table of morphometrics essential for description of the changes in body proportions. These specimens also were used for describing the development of the melanophore pattern and of photophores. A second series of 11 larvae was cleared with KOH and stained with Alizarin Red-S; a table of meristics was constructed from counts made on these specimens.

For purposes of discussion we have included information and illustrations of nine genera related to *Scopelopsis*. These specimens and data, accumulated over an extended period of time, have come largely from the plankton collections of the California Cooperative Oceanic Fisheries Investigations, the NORPAC Expedition, the EASTROPAC Expedition, and the Danish Oceanographic Expedition, in addition to the two sources mentioned above. Where specimens from these and other sources are illustrated, appropriate station data are included in the caption accompanying the figure.

DESCRIPTION OF DEVELOPMENT OF *SCOPELOPSIS MULTIPUNCTATUS*

(Figures 1-3)

LITERATURE

Regan (1916) described the species *Lampanyctus longipinnis* from a 15-mm larval specimen. Judging from the fin counts given in the description and from the somewhat illegible drawing, the specimen was a larva of *Scopelopsis multipunctatus*.

MORPHOLOGY

Larvae of *Scopelopsis* are moderately slender. Body depth at the pectoral fin base is 18-19% of the body length in larvae undergoing notochord flexion and is 20-24% (mean of 22%) in later larval stages and transforming specimens (Table 1). The gut is of moderate length in specimens undergoing notochord flexion; snout-anus length is 44-45% of body length. The gut is conical in these specimens and gradually arches posteriad to the short terminal section. Snout-anus distance increases slightly in later larval and transforming specimens, which have a snout-anus length of 50-54% (mean of 52%) of body length. In these, the gut is covered by trunk musculature.

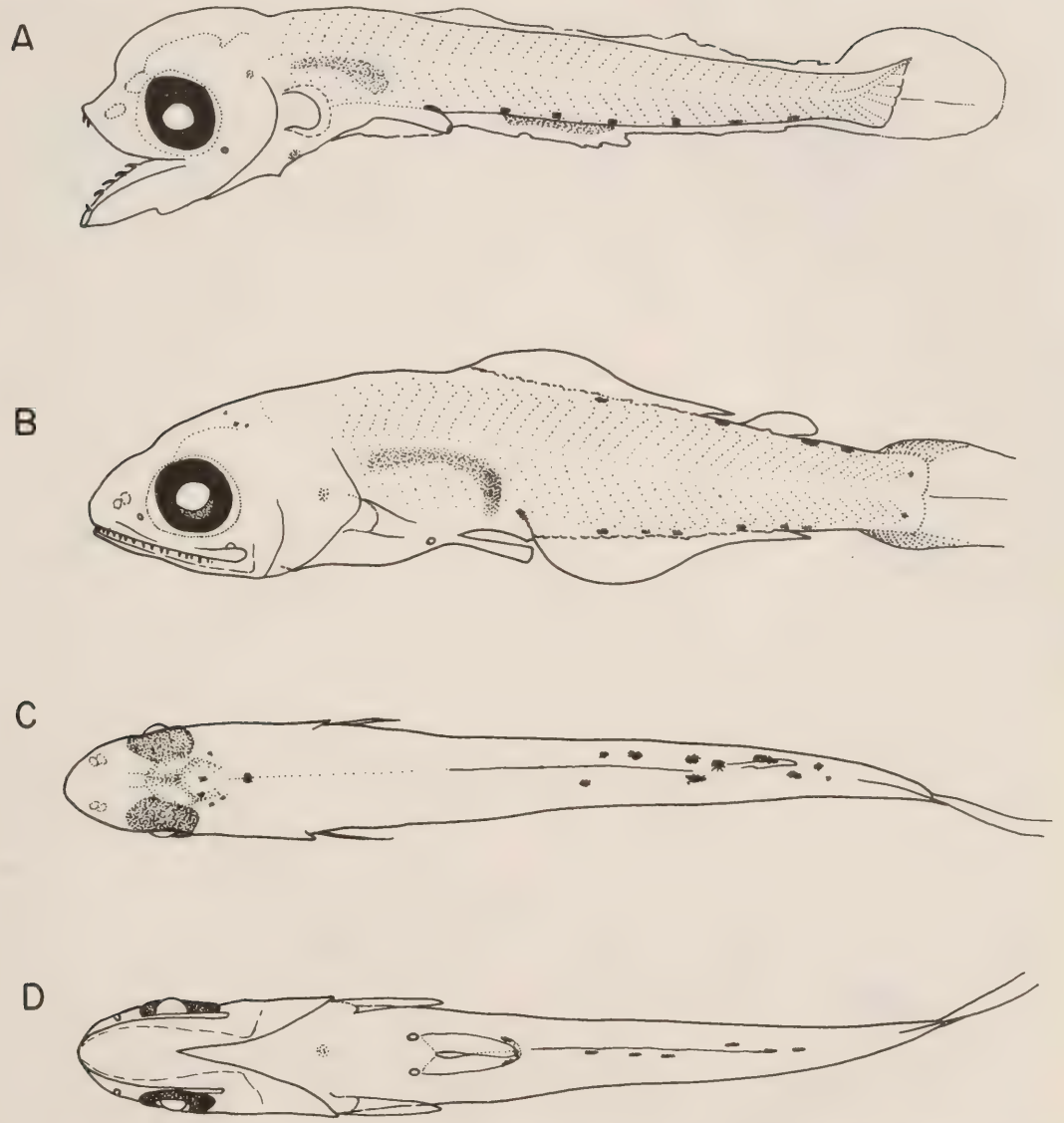

FIGURE 1.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 5.4-mm larva, R.R.S. *Discovery* Station 2352; B, 11.3-mm larva, R.R.S. *Discovery* Station 2352; C, 11.3-mm larva, dorsal view; D, 11.3-mm larva, ventral view.

The head is moderately large, its length being 24-28% (mean of 27%) of the body length for the larval series. The dorsal profile of the snout is concave in our smallest specimen (5.4 mm), but is straight in a 6.2-mm larva, and becomes distinctively bulbous in later larvae and in transforming specimens. The eyes are large in *Scopelopsis* larvae, but undergo a slight diminution, relative to head size, with progressive larval development. Eye length measured vertically is 38% of the head length in the smallest larva, but decreases to 35% in a 6.2-mm larva. This dimension averages 30% of the head length in larvae which have completed notochord flexion,

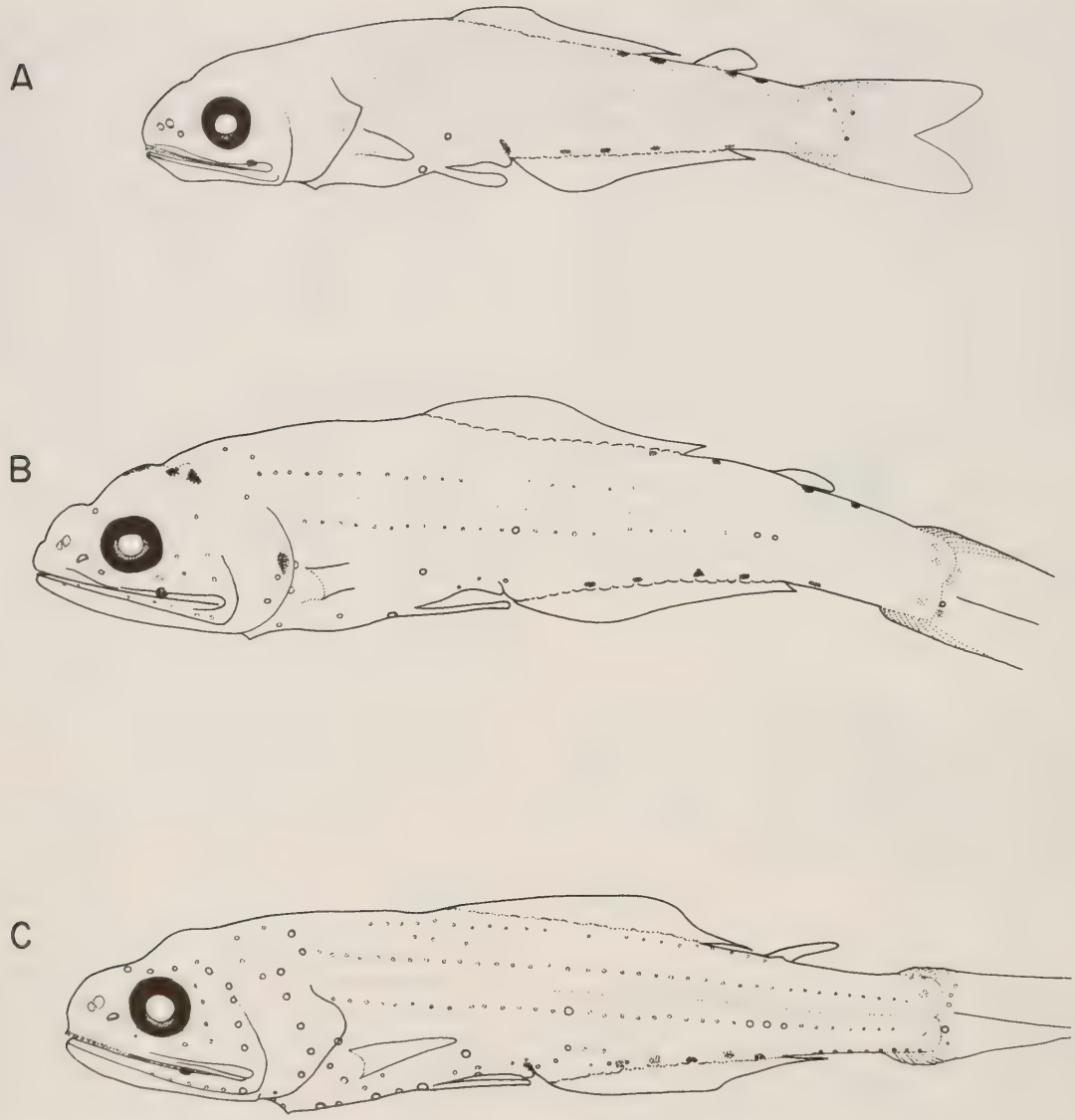

FIGURE 2.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 13.4-mm larva, R.R.S. *Discovery* Station 412; B, 17.6-mm transformation stage, R.R.S. *Discovery* Station 2280; C, 16.7-mm transformation stage, R.R.S. *Discovery* Station, 419.

but this is reduced to an average of 25% in transforming specimens and to 22% in a newly transformed juvenile. The eyes are round or nearly so in *Scopelopsis*; eye width, measured horizontally, averages 92% of eye length for the larval series. In the 17.4-mm juvenile, the horizontal measurement is slightly greater than the vertical. Choroid tissue is absent from the ventral surface of the eye. The initial lateral teeth of the lower jaw are characteristically curved anteriad. Later, the more typical dentary teeth form anterior to the curved teeth; the latter occupy the posterior half of each dentary in larger larvae.

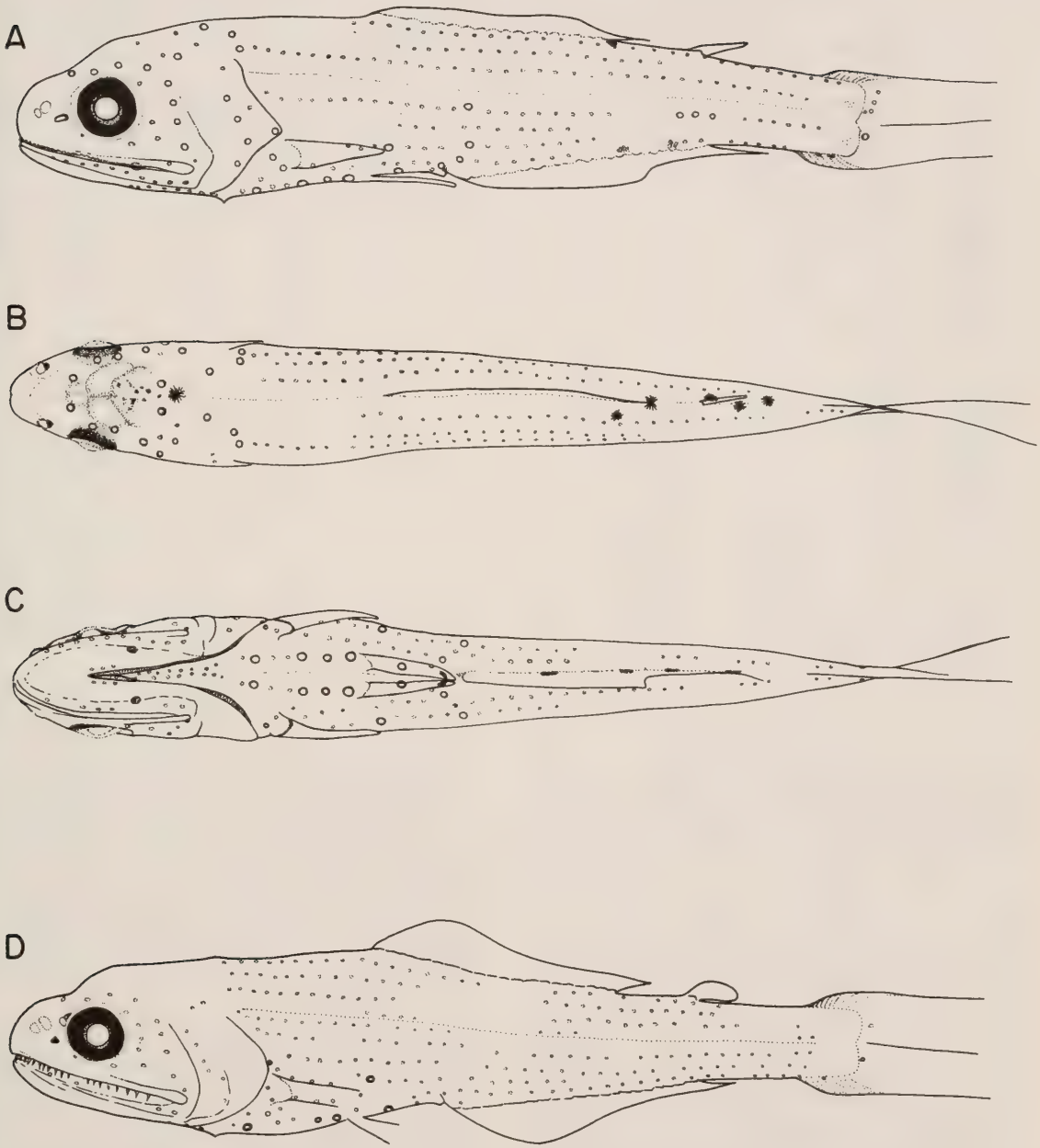

FIGURE 3.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 17.5-mm transformation stage, R.R.S. *Discovery* Station 419; B, 17.5-mm transformation stage, dorsal view; C, 17.5-mm transformation stage, ventral view; D, 17.4-mm juvenile, R.R.S. *Discovery* Station 412.

TABLE 1.—Measurements (mm) of larvae of *Scopelopsis multipunctatus*. (Specimens below dashed line have completed notochord flexion.)

Body length	Snout to anus	Head length	Head width	Inter-orbital width	Body depth at base of pectoral fin	Eye length	Eye width	Snout to origin of anal fin	Snout to origin of dorsal fin	Snout to origin of pelvic fin
5.4	2.4	1.3	0.76	0.46	1.0	0.50	0.43	2.8	--	--
6.2	2.8	1.7	0.87	0.58	1.1	0.59	0.52	3.1	2.8	2.4
10.8	5.4	2.8	1.4	1.2	2.2	0.87	0.81	5.4	4.6	4.1
11.3	5.8	3.2	1.5	1.3	2.5	1.0	0.95	5.8	5.0	4.6
12.2	6.4	3.2	1.6	1.3	2.7	1.0	0.90	6.4	5.2	4.8
12.3	6.3	3.2	1.6	1.3	2.6	0.94	0.86	6.3	5.2	4.8
12.4	6.5	3.3	1.7	1.4	2.6	1.0	1.0	6.5	5.4	5.0
12.8	7.1	3.3	1.8	1.4	3.0	1.1	1.0	7.1	5.6	5.4
13.0	6.8	3.4	1.7	1.4	2.8	1.0	0.95	6.8	5.7	5.2
13.1	7.1	3.4	1.8	1.5	3.1	1.0	0.91	7.1	5.8	5.3
13.2	6.7	3.2	1.8	1.5	2.8	0.97	0.83	6.8	5.5	5.2
13.4	7.0	3.6	2.1	1.5	3.1	1.0	0.87	7.0	5.8	5.3
13.5	6.9	3.5	1.8	1.4	2.8	1.1	0.91	6.9	5.8	5.2
13.8	7.4	3.7	1.8	1.4	2.8	1.1	1.0	7.4	6.1	5.5
13.9	6.9	3.5	1.8	1.5	2.9	1.0	0.92	6.9	5.9	5.3
14.2	7.4	3.8	2.0	1.5	3.2	1.0	0.95	7.4	6.2	5.7
14.3	7.4	3.7	1.8	1.4	3.1	1.0	0.95	7.4	6.2	5.5
14.6	7.4	3.8	1.8	1.7	3.2	1.1	1.0	7.4	6.2	5.4
14.9	7.8	4.2	2.0	1.7	3.2	--	--	7.8	--	6.1
15.2	8.2	4.2	1.9	1.7	3.3	--	--	8.2	7.0	6.2
15.5	8.2	4.4	2.0	1.7	3.4	--	--	8.2	7.0	6.2
[1]16.7	8.8	4.6	2.3	1.9	3.8	1.2	1.1	8.8	7.0	6.7
[1]17.5	8.8	4.8	2.5	1.8	3.6	1.2	1.2	8.8	7.2	6.9
[1]17.7	8.8	4.8	--	--	3.8	1.2	1.2	--	7.4	6.7
[2]17.4	9.0	4.9	2.4	1.9	3.7	1.1	1.2	9.0	7.2	6.9

[1] Transformation stage.
[2] Juvenile.

FIN DEVELOPMENT

Our smallest specimen (5.4 mm) is undergoing flexion of the tip of the notochord and already has the adult complement of 10 superior and 9 inferior principal caudal rays (Table 2). In the next smallest larva (6.2 mm), also undergoing notochord flexion, a single procurrent ray is forming in the superior and inferior series. The adult complement of 10-11 superior and 10-12 inferior procurrent rays is present in larvae 13.0 mm and larger.

The pectoral fins are represented by their inconspicuous bases in the 5.4- and 6.2-mm specimens; the fins themselves are membranous, with no ossified rays. Description of the gradual acquisition of ossified rays described for pectoral fins of other species (Moser and Ahlstrom, 1970) is precluded by the gap in our series of *Scopelopsis*. Larvae 10.8 mm and larger have the adult complement of 10-11 rays in each fin.

The bases of the dorsal and anal fins are beginning to form on the 5.4- and 6.2-mm larvae, but no rays are ossifying. Larvae 10.8 mm and larger have the adult complement of 21-23 dorsal and 23-25 anal rays.

The pelvic fin buds are present in the 6.2-mm larva, and larvae 10.8 mm and larger have the adult number of 8 rays in each fin. The adipose fin is beginning to develop at 6.2 mm and is well formed by 10.8 mm.

Gill rakers and vertebrae develop later than do the fins. Gill rakers are first apparent in the 10.8-mm larva and are added gradually. On the first arch, the full complement of 7-9 epibranchial rakers is achieved at 13.5 mm while, on the lower limb of the arch, the full complement of 15-17 rakers is present at 15.2 mm. A 10.8-mm larva already has 34 vertebral centra forming; the adult number of 37-40 vertebrae is present in larvae 12.2 mm and larger.

TABLE 2.—Meristic characters of cleared and stained larvae of *Scopelopsis multipunctatus*.

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper left limb	Lower right limb			Left	Right	
5.4	10	9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6.2	10	9	1	1	--	--	--	--	--	1	--	--	--	--	--	--	--
10.8	10	9	9	10	8	8	11	11	4	3	4	12	24	23	8	8	34
12.2	10	9	9	10	9	9	10	10	4	3	6	12	24	22	8	8	39
13.0	10	9	10	11	10	10	10	11	4	3	6	14	23	21	8	8	38
13.5	10	9	11	12	9	9	10	10	4	3	7	14	24	22	8	8	39
13.9	10	9	10	12	9	9	11	11	4	3	7	14	25	23	8	8	39
14.3	10	9	11	12	9	10	11	11	4	3	7	14	24	22	8	8	38
15.2	10	9	11	11	10	10	11	12	4	3	8	16	24	22	8	8	39
15.7	10	9	9	11	10	10	11	10	4	3	8	15	23	22	8	8	39
17.6	10	9	10	12	10	10	10	11	4	3	8	16	24	23	8	8	39

PIGMENTATION

Scopelopsis larvae develop a distinct pattern of melanophores. The smallest larva in our series (5.4 mm) has a prominent median melanophore at the nape and a smaller melanophore embedded in the otic region at each side of the head. Another large melanophore is embedded at the ventral midline, just below the bases of the pectoral fins. An equally prominent melanophore lies above the gut, at the point where the free terminal section diverges from the body. An elliptical shield of melanophores lies above the developing gas bladder but is partially masked by the body wall musculature. A series of six evenly spaced melanophores is embedded along the ventral midline of the tail. All the melanophores that constitute this initial pattern remain throughout the larval period. The series at the ventral midline of the tail usually contains five or six melanophores in older larvae; specimens with fewer than three or more than eight were not found.

Another major area of pigmentation is visible in a 6.2-mm larva, which has two melanophores in the dorsal midline posterior to the adipose fin. In larger larvae this series extends anterior to the dorsal fin, with the usual condition being a series of three, four, or five melanophores on, or on either side of, the midline. An 11.3-mm larva has the maximum number of 10 melanophores in this series, with several of the melanophores positioned along the base of the dorsal fin.

Final additions to the melanophore pattern are in the head and caudal fin. In specimens 10.8 mm and larger, a melanophore is embedded anterior to the base of each pectoral fin, and specimens 11.3 mm and larger have one to several melanophores above the posterior region of the brain. Larvae 10.8 mm and larger have one to several melanophores embedded in the hypural region of the tail; these melanophores may lie over the superior hypurals, the inferior elements, or both. Similarly, in specimens 12.3 mm and larger, one to several melanophores may be found at the base of the caudal rays, either at the superior group, the inferior group, or both. Some specimens lack these caudal ray melanophores. A few larvae have an additional median melanophore at the junction of the hypural elements and the rays.

PHOTOPHORE DEVELOPMENT

A number of photophores develop in larvae of *Scopelopsis* in a prescribed sequence.[2] As in most other myctophids the Br_2 are the first to form. They are just visible in our smallest specimen (5.4 mm) and are well formed in a 10.8-mm specimen. The next to appear is the posteriormost PO pair which is just visible in the 10.8-mm larva but is well formed, although small, in

[2] For clarity, a diagram of the characteristic photophore groups of adult myctophids is shown in Figure 4.

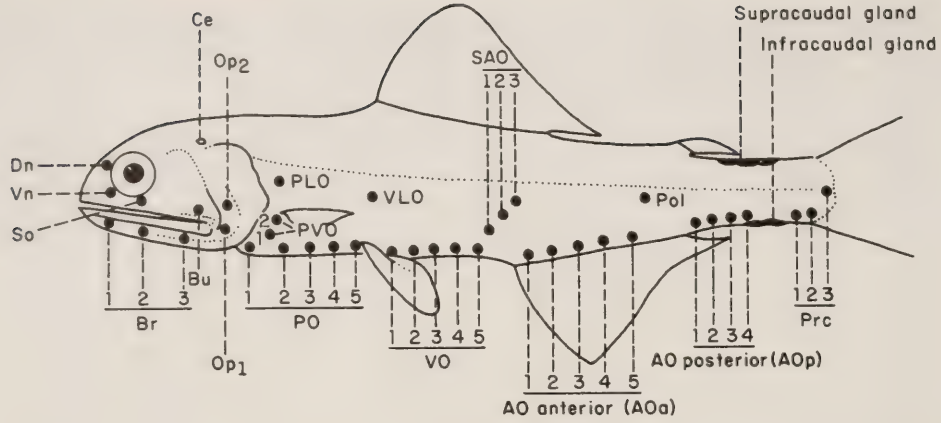

FIGURE 4.—Diagram of characteristic photophore groups of adult myctophids (modified from Nafpaktitis and Nafpaktitis, 1969 and Fraser-Brunner, 1949).

larger specimens in the series. The next to develop are the Vn; they appear anteroventral to the eye in the 11.3-mm larvae and become progressively cup-shaped as development proceeds. At the end of the larval period they are the largest photophores present. During transformation they begin to be overlain with tissue and bone so that they are difficult to see in juveniles and adults; this is doubtless why they have been overlooked by recent authors (Fraser-Brunner, 1949; Nafpaktitis and Nafpaktitis, 1969). The fourth pair of photophores to develop are the VLO; they first appear slightly posterior to, but well above, the bases of the pelvic fins in a 13.4-mm larva.

The four pairs of photophores described above are the only ones to develop until the larvae reach about 15-mm length. In a series of five larvae 14.9-15.7 mm long, a number of other photophores are beginning to appear. In the jaw region one is visible just below the terminus of each maxillary, and another is forming above and slightly anterior to the end of the maxillary. One or two others are developing in a line extending dorso-anteriad from the latter cheek organ. Dorsally on the head, a photophore is developing above the lateral margin of each olfactory lobe. In the PO series two pairs are evident, one slightly posterior to the juncture of the cleithra and another pair equidistant between this pair and the most posterior pair, described above. A VO pair is developing midway between the bases of the pelvic fins and the anus. Farther posterior on the body, the SAO_3 are developing as are the posteriormost Prc pair.

The photophore pattern is augmented further in the three remarkable transforming specimens illustrated in Figures 2 and 3, in which the adult pattern of photophores is clearly emerging. The three represent a developmental series of which the 17.6-mm specimen is the least advanced, followed by the progressively more advanced 16.7- and 17.5-mm specimens. In the 17.6-mm specimen the previously described photophore pattern on the head is augmented by several organs below and to the rear of the eye, by a line of organs along the lower jaw, and by several on the opercle. On the body a PLO and one PVO is present at the pectoral fin base, several organs are forming above the vent, and two POL are arranged horizontally above the end of the anal fin. In addition, two horizontal lines of photophores are beginning to appear, one above and one below the lateral line. The adult photophore arrangement of *Scopelopsis* is clearly manifest in the 16.7- and 17.5-mm specimens. Photophores are beginning to cover the head in a definite pattern; some of these are considerably larger and more defined than others. On the body the many regular rows of secondary organs are emerging, al-

though the following larger and more distinct primary photophores stand out on the 17.5-mm specimen: PO_{1-4}, $PVO_{1 \text{ and } 2}$, VLO, VO, SAO_{1-3}, POL_{1-3}, Prc.

In the 17.4-mm juvenile it is evident that the photophores on the body are on the posterior margin of each scale pocket, thus explaining their regular arrangement into horizontal rows. The specimen is partially skinned, but one can see that some body photophores remain decidedly larger than others (notably two of the PO, the VLO, and VO), while generally the distinction between primary and secondary organs is less marked. On the head, certain of the cheek photophores remain large and distinct and, additionally, the two-part Dn is now present as are the small anterior and posterior Br.

Opinion has been divided on whether or not the dichotomy of primary and secondary photophores, described above, is present in adult *Scopelopsis*. In his original description Brauer (1906) did not distinguish between primary and secondary organs. Tåning (1932) stated that some of the organs were larger than others and, moreover, made the important observation that the scales over these larger organs were equipped with a special lenslike modification typical of other myctophids. He noted that among the prominent photophores were a PLO, two PVO, a VLO, three SAO in a rather steep line, and two POL in a horizontal line. His statement, " . . . in fact we find all the different groups of organs which we have in all other species of the subfamily Myctophini, small, but larger than the very small organs scattered all over the body . . ." was unaccompanied by an illustration. Fraser-Brunner (1949) recognized that certain photophores were more highly developed than others and termed these primary organs in contrast to the less highly developed secondary organs. He gave the following formula: "PLO above, both PVO below base of pectoral. Five PO. Five VO. Three SAO in an oblique series. AO in two series. Two POL in horizontal series. Five or more Prc." His accompanying illustration shows the basic photophore pattern but is somewhat illegible, especially in the caudal region. Nafpaktitis and Nafpaktitis (1969) could not differentiate primary and secondary photophores in their material. Wisner (in press) employed a large series of excellently preserved specimens in his description of *Scopelopsis* and showed that the ability to differentiate primary from secondary photophores is dependent on the condition of the specimen. In specimens which had retained most of their scales he identified primary photophores as those with a lenslike modification of the overlying scale. His photophore formula and clear illustration corroborate the observations of Tåning (1932) and Fraser-Brunner (1949); further refinements include his observation of 7-10 anterior AO, 5-6 posterior AO, 4-6 Prc, 2 or 3 POL, and 3 prominent cheek photophores in a diagonal line anterior to the preopercle. Additionally he shows definitively the two-part Dn and the embedded Vn. The observations of Tåning (1932), Fraser-Brunner (1949), and Wisner (in press) along with the evidence presented herein demonstrate that certain of the multitudinous light organs of *Scopelopsis* are more highly developed than others and that these "primary organs" are arranged in a pattern that corresponds to the general pattern of other members of the family. Our observations on ontogenetic series largely confirm the arrangement of primary photophores postulated by these authors, but some of our findings suggest discrepancies that may only be clarified by further examination of undamaged adults. For example, we find only four well-developed PO and a single large VO in transforming specimens and in juveniles and adults available to us. This as well as the exact frequencies of AO and Prc series await elucidation by workers with large series of intact adults.

SYSTEMATIC RELATIONSHIPS

The efficacy of using the larval and transformation stages of lanternfishes to elucidate specific and supraspecific relationships has been clearly demonstrated (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1970). We (Moser and Ahlstrom, 1970) showed that the genera of Myctophidae can be divided into two groups on the basis of larval eye shape—those with narrow elliptical eyes and those with round or nearly

round eyes. That these are phylogenetically natural groups is supported by Paxton (1968, 1972) who, on the basis of adult osteology and photophore arrangement, formally established the same two groups of genera as subfamilies. He grouped the 11 genera with narrow-eyed larvae into the subfamily Myctophinae and the 17 genera with round-eyed larvae into the subfamily Lampanyctinae. Further, in our paper we described the evolutionary lineages within the Myctophinae as evidenced by the structure of the larvae. Many of our conclusions agreed with those of Paxton (1968), derived from adult characters, but we differed ultimately with his distribution of the 11 myctophine genera into two tribes and with his derivation of the subfamily Lampanyctinae from an already highly evolved lineage of the subfamily Myctophinae. The larvae of the subfamily Lampanyctinae, although morphologically conservative compared with those of the Myctophinae, are useful, nonetheless, in revealing evolutionary lineages within the subfamily. The diversity of eye shape, so spectacular in the Myctophinae, is absent in the Lampanyctinae, but the eyes of many genera are distinctive because of their size, subtle but characteristic deviation from the basic rounded outline, or presence of a ventral crescent of choroid tissue. Likewise each genus of Lampanyctinae has a characteristic body shape, although the subfamily lacks the diversity of body form, so dramatic in the Myctophinae. The peculiar modifications of the paired fins, common among the larvae of Myctophinae, are generally absent in the Lampanyctinae; only in the lampanyctine genera *Lampanyctus* and *Lobianchia* do the pectoral fins attain some degree of specialization.

Three characters that are shared by the larvae of many lampanyctine genera are: 1) the sequential development of three or more pairs of early-forming photophores, 2) the development of a series of melanophores at the dorsal and at the ventral margins of the body, particularly in the tail region, and 3) the development of one or more melanophores above the brain. The sequence of development of early-forming photophores is an especially useful character that may provide a key to the elucidation of phylogenetic lineages within the Lampanyctinae. Eleven of the 17 genera of Lampanyctinae develop such early-forming photophores and can be grouped as follows:

Group A—Br_2, PO_5, and Vn form in that sequence; fourth pair, either PLO or VLO, form later in larval period.
- *Scopelopsis* - VLO fourth pair to form.
- *Notoscopelus* - PLO fourth pair to form.
- *Lampichthys* - PLO fourth pair to form.

Group B—Br_2, Vn, PLO, and PO_5 form sequentially; photophores very small.
- *Ceratoscopelus* - all four pairs formed early in larval period.
- *Bolinichthys* - some species develop larval photophores, as above, and others develop only the Br_2 as larvae.
- *Lepidophanes* - Vn, PLO, and PO_5 form almost simultaneously after the Br_2; OP_1, and OP_2 form just before transformation.

Group C—Br_2, PLO, and PO_5 early-forming.
- *Lampadena* - Br_2, PLO, and PO_5 appear sequentially; later in larval period, PO_1 and Vn form sequentially.
- *Lampanyctodes* - Br_2, PLO, and PO_5 formed on 9.2-mm larva; smaller larvae and, consequently, information on sequence of appearance, not available.

Group D—Br_2, PO_5, and PO_1 early-forming.
- *Gymnoscopelus* - Br_2, PO_5, and PO_1 form sequentially, early in the larval period; much later, the VO_1 and then PO_2 appear.
- *Diaphus* - two species groups; *D. theta* and relatives form Br_2, PO_5, PO_1, VO_1, PO_2, OP_2, VO_5, PO_3, PO_4, VLO sequentially; *D. pacificus* and relatives form Br_2, PO_5, PO_1, PO_2, PVO_1, PO_3, VO_1, sequentially; photophores added gradually in *Diaphus* larvae with transformation at small size.
- *Lobianchia* - Br_2, PO_1, PO_5, PVO_1, PVO_2 form sequentially.

The above groupings suggest phylogenetic affinities which, in most cases, are supported by other characters of the larvae and adults. The sequential development of the Br_2, PO_5, and Vn photophores is unique to the genera of Group A (*Scopelopsis, Lampichthys, Notoscopelus*). The arrangement of primary photophores, so conspicuous in the transforming specimens of *Scopelopsis*, affirms the close relationship of this genus

with *Notoscopelus* and *Lampichthys*, since the three genera are the only myctophids with horizontal POL photophores on the posterior lateral surface of the body. *Scopelopsis* and *Notoscopelus* have either two or three such photophores in a horizontal line below the lateral line, while in *Lampichthys* the two horizontal photophores form a right angle with a third POL that is placed midway between the two upper POL's and the ventral series. Other characters of the larvae substantiate the close relationship of these three genera. The larvae are similar in shape of the eye, head, and body. *Scopelopsis* and *Lampichthys* have extremely similar pigment patterns and differ only in the number and size of the melanophores in each area (Figures 1-3, 5). *Notoscopelus* differs only slightly from the other two, in its lack of a melanophore in the ventral midline below the pectoral fin and in having a prominent series of melanophores along the lateral line (Figure 6).

Characters of the adults affirm the close relationship of the three genera. *Scopelopsis* and the several species of *Notoscopelus* have the highest numbers of dorsal fin rays, 21-23 and 22-27 respectively, in the family. The Dn light organ at the anterodorsal margin of the orbit is composed of two contiguous structures in *Scopelopsis* and *Notoscopelus*; it consists of a small photophore, with a margin of black pigment, dorsal to a larger opaque mass of tissue that lacks marginal pigment. In *Lampichthys* a mass of black tissue lies below the opaque luminous tissue, which extends posteriad over the entire dorsal surface of the orbit. *Scopelopsis* is covered entirely by small secondary photophores, as is the body of *Lampichthys*. Such photophores are absent from the head of *Lampichthys;* however, the four or five prominent cheek photophores of *Lampichthys* are comparable to those of *Scopelopsis*. A single opaque patch of luminous tissue lies below each pectoral fin base in *Scopelopsis*. In *Lampichthys*, a luminous patch is present in exactly the same position; however, several additional patches are present on the lateral surfaces of the body. In *Notoscopelus*, luminous patches are much more extensive, although the prominent patch below the base of each pectoral fin is present in all species of the genus.

The sequential development of the Br_2, Vn, PLO, and PO_5 is unique to the genera in group B (*Ceratoscopelus, Lepidophanes, Bolinichthys*); this, along with the small size of the photophores, and their early appearance, points to close relationship of the three genera. The larvae of some species of *Bolinichthys* are an exception, since they develop only the Br_2. Other characters of the larvae, such as a similarity in body shape and a general paucity of pigment, also suggest the close relationship of the three genera (Figures 7, 8, 9). Paxton (1972) has pointed out a number of osteological characters of the adults that link the three genera, and the similarity in the arrangement of luminous patches among species of the three genera is well established in the literature.

The larvae of *Lampadena* and *Lampanyctodes* (group C above) develop the Br_2, PLO, and PO_5. The PLO photophores become conspicuously developed on small larvae of *Lampadena* soon after the formation of the Br_2 pair; the PO_5 pair appear shortly thereafter (Figure 10). The Vn pair is later-forming and may be preceded by the PO_1 pair, or the two pairs may form simultaneously. The sequence of development of early-forming photophores on *Lampanyctodes hectoris* has not been fully established. The Br_2, PLO, and PO_5 pairs were well developed on the smallest larva (9.2 mm) available for study (Figure 11). A 14.5-mm transforming specimen of *Lampanyctodes* had 13 pairs of photophores developed, including the Vn and PO pairs. Even so, the only genera with this combination of three early-forming photophores are *Lampadena* and *Lampanyctodes*. Also, the larvae of the two genera are similar in body shape and in pigmentation.

The larvae of *Gymnoscopelus* (group D above) form the Br_2, PO_5, and PO_1 early (Figure 12). Later in the protracted larval period, the VO_1 and then PO_2 appear. In some species (e.g., *G. aphya*) the larvae reach a length of 28 mm and are the largest of all myctophid larvae. *Diaphus* and *Lobianchia* also develop the Br_2, PO_5, and PO_1 early in the larval period and are included in group D. This, however, is virtually the only larval character that the two genera share with *Gymnoscopelus*. They develop photophores grad-

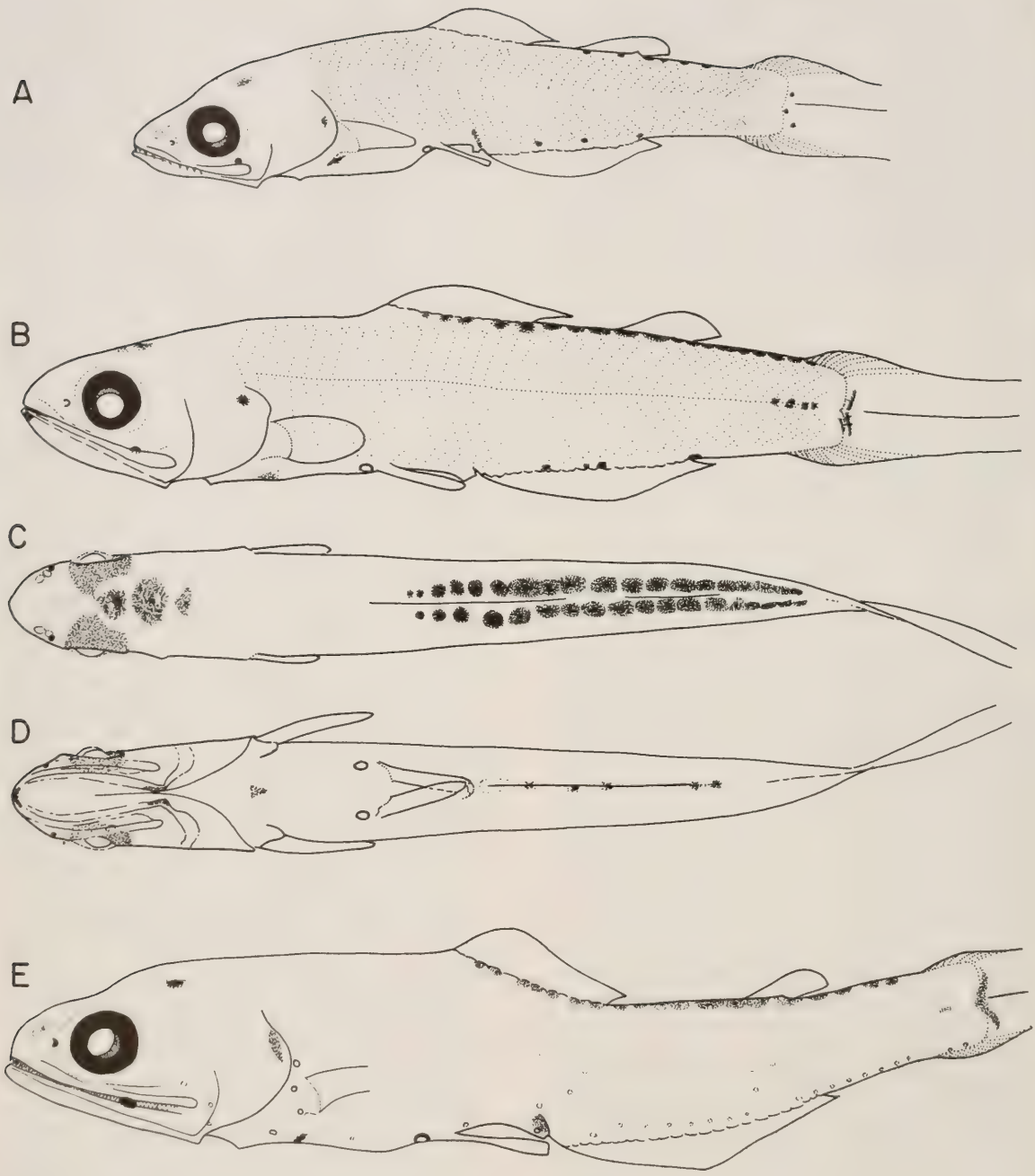

FIGURE 5.—Developmental stages of *Lampichthys procerus* (Brauer).—A, 11.4-mm larva, U.S. NS *Eltanin* Station 314; B, 14.5-mm larva, R.R.S. *Discovery* Station 100c; C, 14.5-mm larva dorsal view; D, 14.5-mm larva, ventral view; E, 20.3-mm transformation stage, U.S. NS *Eltanin* Station 306.

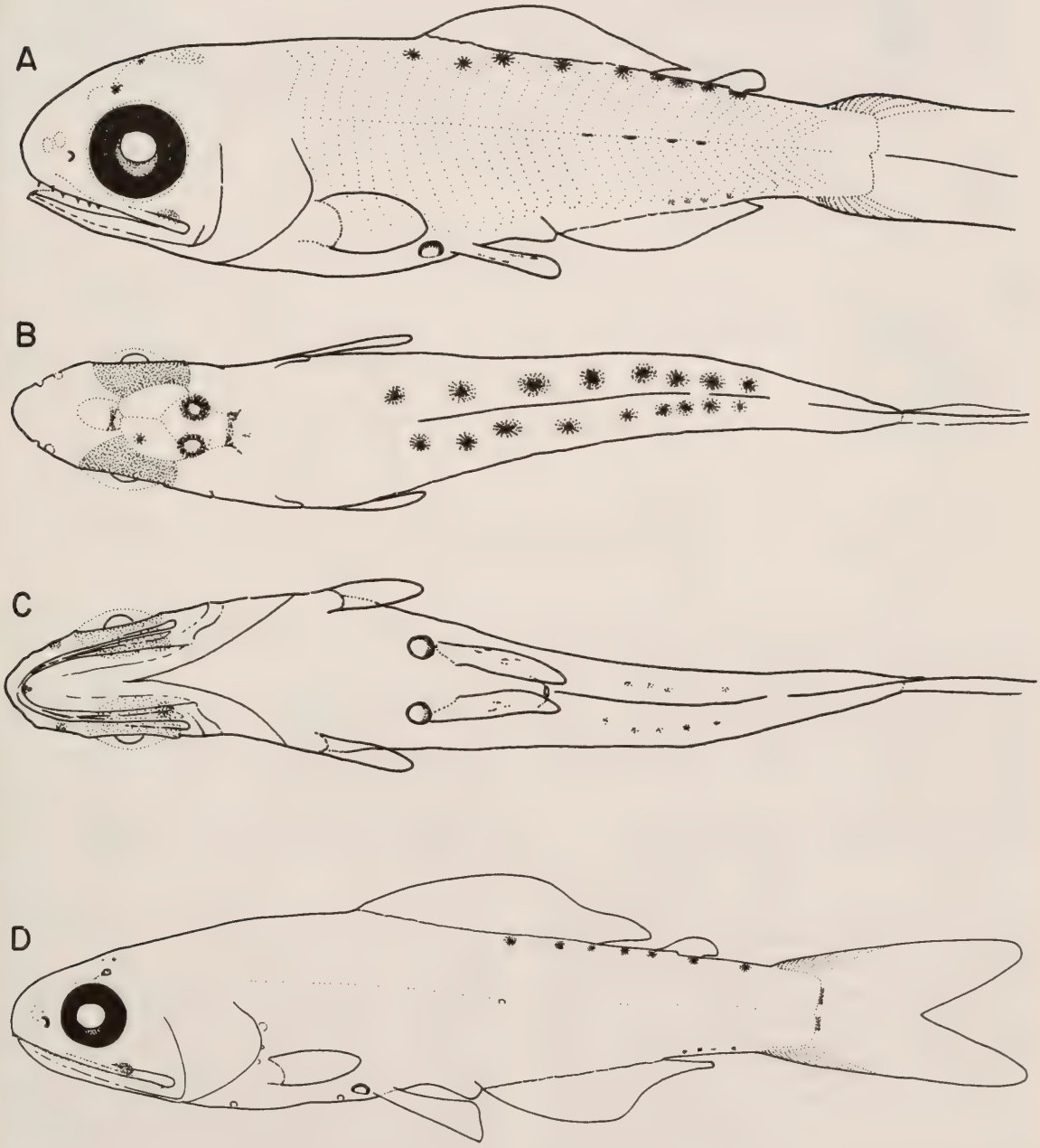

FIGURE 6.—Developmental stages of *Notoscopelus resplendens* (Richardson).—A, 11.2-mm larva, CalCOFI 6310-97.90; B, 11.2-mm larva, dorsal view; C, 11.2-mm larva, ventral view; D, 21.0-mm transformation stage, CalCOFI 6207-90.110.

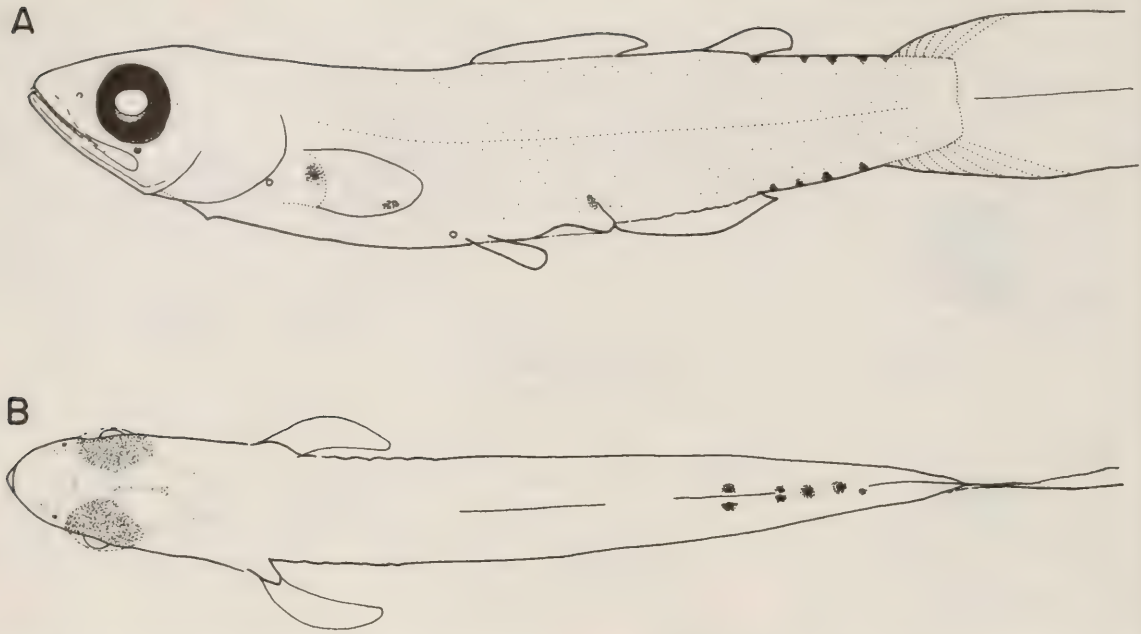

FIGURE 7.—Developmental stage of *Ceratoscopelus maderensis* (Lowe).—A, 13.4-mm larva, RV *Meteor* Station 72-39; B, 13.4-mm larva, dorsal view.

ually during the larval period, which appears to be rather short; most species transform within the size range of 10-15 mm. Also, the characteristic shape and basic pigment pattern of larval *Diaphus* and *Lobianchia* are distinctively different from those of *Gymnoscopelus*. In shape and pigmentation, the larvae of *Gymnoscopelus* resemble most closely those of group A (*Scopelopsis, Lampichthys, Notoscopelus*).

Of the remaining six genera of the subfamily Lampanyctinae, *Notolychnus* develops no photophores during the larval period, and *Lampanyctus, Triphoturus,* and *Stenobrachius* develop only the Br_2 as larvae. Our developmental series of *Taaningichthys* is incomplete; however, larvae up to 18 mm long have no photophores. In our largest larva (19.3 mm), the PO_5 are just beginning to develop. The larvae of this genus are apparently neustonic, and this may have an important influence on photophore development. They are most similar to larvae of *Lampadena* in pigment pattern but are much more slender. The small larvae of *Taaningichthys minimus* are unusual in having a conspicuous series of embedded melanophores above the vertebral column (Figure 13). The larvae of *Hintonia* are as yet unknown.

From our studies of the larvae of the subfamily Lampanyctinae, the genera *Scopelopsis, Lampichthys, Notoscopelus, Gymnoscopelus, Ceratoscopelus, Bolinichthys, Lepidophanes, Lampanyctodes, Lampadena,* and *Taaningichthys* emerge as a natural assemblage based on sequence of photophore development, morphology, and pigmentation. The grouping of these genera as a phylogenetic unit conflicts with the phylogenetic scheme proposed by Paxton (1968, 1972). His arrangement of the 17 genera of the subfamily Lampanyctinae into four tribes, based on a combination of adult osteology and photophore pattern, is shown in Figure 14. We agree that *Notolychnus valdiviae* has an ample array of unique adult and larval characters to warrant its placement in the monotypic tribe Notolychnini. Likewise we concur with the establishment of a separate tribe Diaphini for *Diaphus* and *Lobianchia,* two genera with a dis-

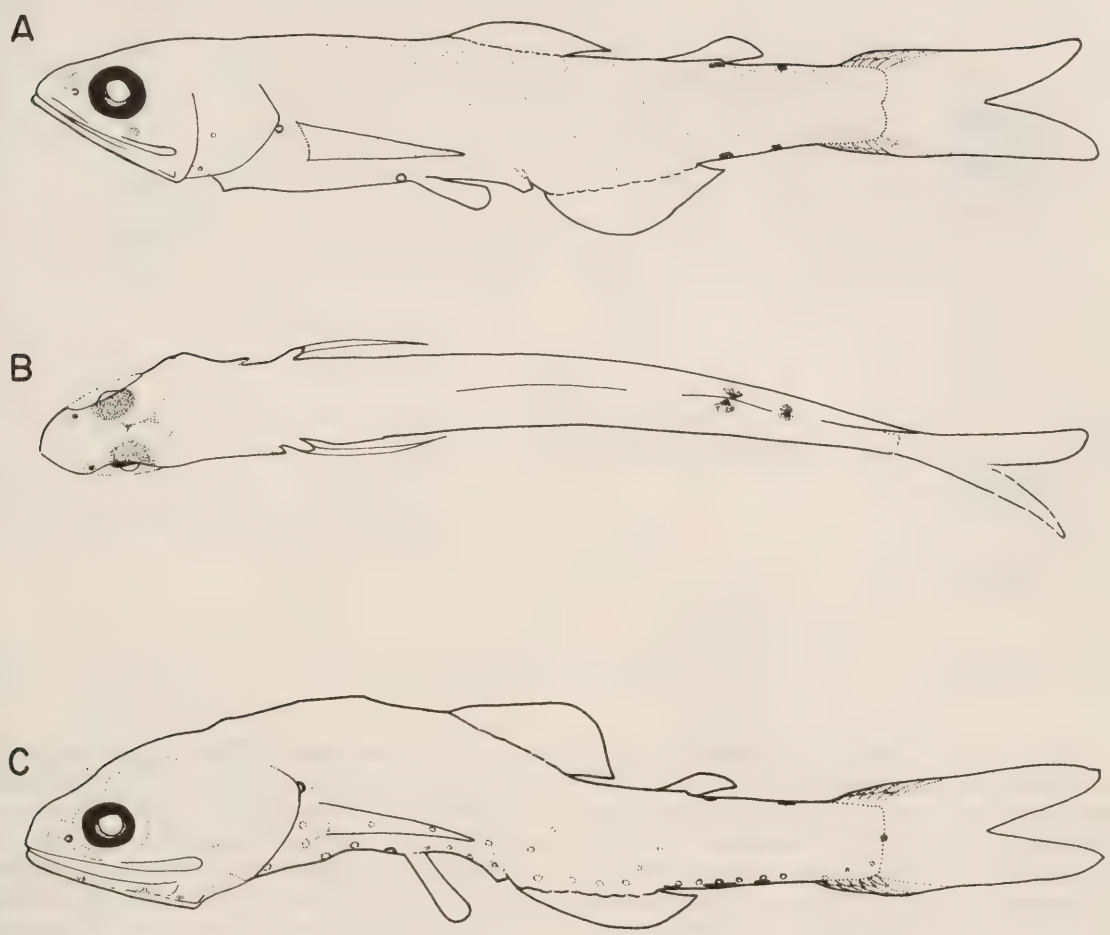

FIGURE 8.—Developmental stages of *Lepidophanes guentheri* (Goode and Bean).—A, 13.5-mm larva, R.S. *Dana* Station 3998X; B, 13.5-mm larva, dorsal view; C, 12.7-mm transformation stage, R.S. *Dana* Station 3998X.

tinct facies of adult and larval characters. Paxton placed the remaining 14 genera into two tribes, the Lampanyctini and Gymnoscopelini. On the basis of larval characters, we cannot concur with his distribution of genera among the two tribes. He included eight genera (*Lampanyctus, Stenobrachius, Triphoturus, Ceratoscopelus, Lepidophanes, Bolinichthys, Taaningichthys,* and *Lampadena*) in the tribe Lampanyctini and restricted the tribe Gymnoscopelini to six genera (*Gymnoscopelus, Lampanyctodes, Notoscopelus, Lampichthys, Scopelopsis,* and *Hintonia*). Paxton found no single character that would differentiate any of the four tribes from all others in the subfamily and relied on a combination of osteological and photophore characters to define the tribes. His most trenchant characters separating the Gymnoscopelini from the Lampanyctini were the presence of a supramaxillary bone in the Gymnoscopelini and its absence in the Lampanyctini and the presence of a Dn photophore in the former and its absence in the latter.

Our findings in the larvae suggest a different distribution of genera for the two tribes. On the basis of larval characters described earlier

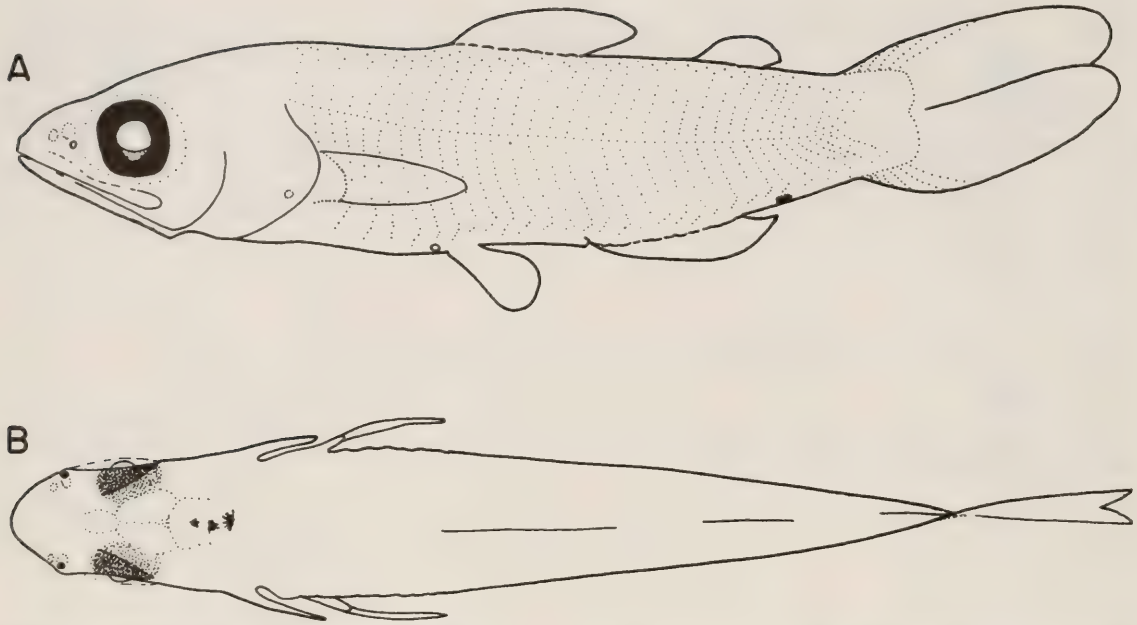

FIGURE 9.—Developmental stage of *Bolinichthys* sp.—A, 10.6-mm larva, R.R.S. *Discovery* Station 702; B, 10.6-mm larva, dorsal view.

we would enlarge the tribe Gymnoscopelini to include *Ceratoscopelus, Lepidophanes, Bolinichthys, Lampadena,* and *Taaningichthys* as well as the six genera assigned to the tribe by Paxton. We would restrict the tribe Lampanyctini to *Lampanyctus, Stenobrachius,* and *Triphoturus,* three genera with distinctive larvae that develop only the Br_2 photophores, and are characterized by an abrupt transformation from larva to juvenile. Our suggested modification of Paxton's scheme is shown in Figure 15.

Even though we propose a different distribution of genera in the tribes Gymnoscopelini and Lampanyctini, there is a striking concordance between our groupings of related genera and Paxton's, derived from quite different criteria. For example, both methods suggest a close relationship for *Scopelopsis, Lampichthys,* and *Notoscopelus* as well as for *Ceratoscopelus, Lepidophanes,* and *Bolinichthys.*

It should be noted that the heaviest development of accessory luminous tissue occurs in the genera we place in the tribe Gymnoscopelini and that such luminous tissue is best developed on *Ceratoscopelus, Bolinichthys, Lepidophanes, Lampichthys,* and *Hintonia.* On *Ceratoscopelus townsendi* and various species of *Bolinichthys,* conspicuous patches of luminous tissue form on the head between the orbits, especially in adult males. In these genera there may be a direct relation between the absence of the Dn photophores and the presence of accessory luminous tissue on the head.

A PROPOSED THEORY FOR THE EVOLUTION OF PHOTOPHORE PATTERN IN MYCTOPHIDAE

Perhaps the most intriguing result of our studies of larvae of the tribe Gymnoscopelini is a theory for the evolution of photophore pattern in lanternfishes. The only previous theory was proposed by Bolin (1939) and fully developed by Fraser-Brunner (1949). Fraser-Brunner (1949) postulated an hypothetical ancestral myctophid with a pair of continuous photophore rows on the ventral margin, beginning with the

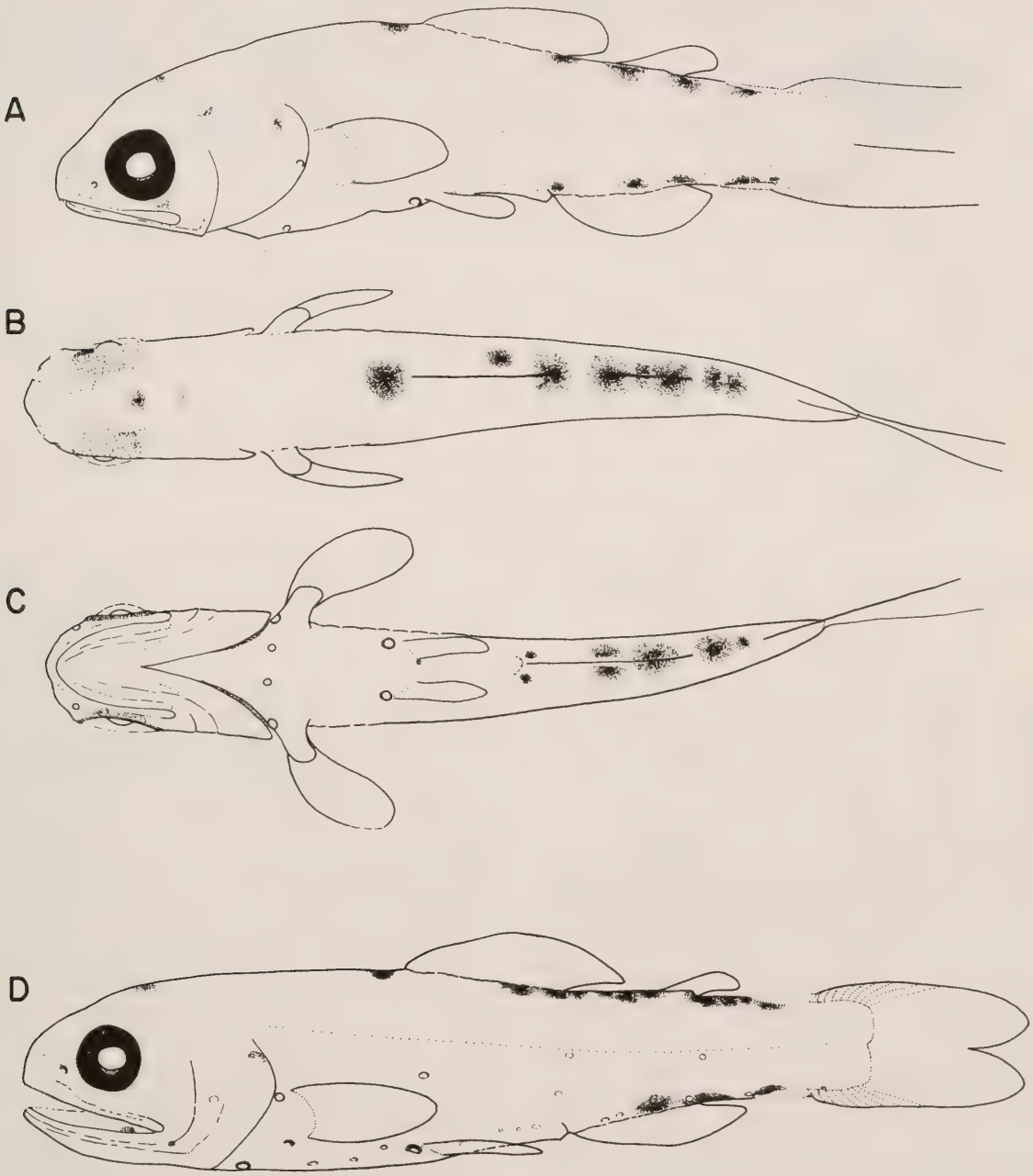

FIGURE 10.—Developmental stages of *Lampadena urophaos* Paxton.—A, 13.4-mm larva, CalCOFI 5011- S-T3; B, 13.4-mm larva, dorsal view; C, 13.4-mm larva, ventral view; D, 19.6-mm transformation stage, CalCOFI 6210-117.90.

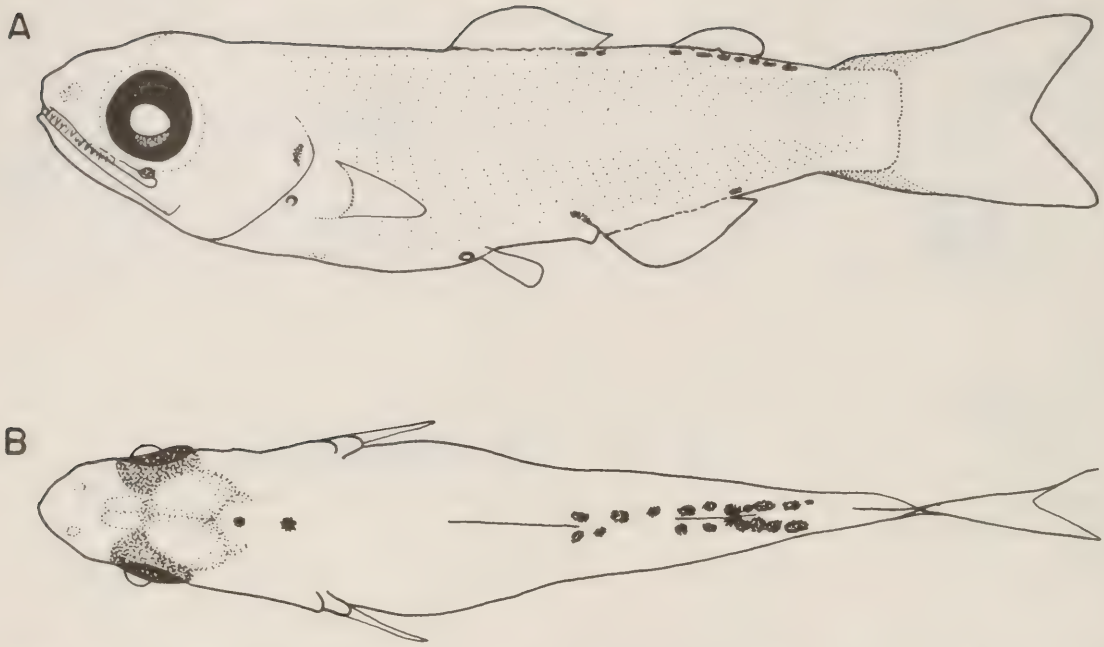

FIGURE 11.—Developmental stage of *Lampanyctodes hectoris* (Günther).—A, 9.2-mm larva, R.R.S. *Discovery* Station 1374; B, 9.2-mm larva, dorsal view.

most ventral jaw photophore (Br_3) and extending posteriad to the tail. Above these ventral rows on each side was a lateral row that extended from the middle jaw photophore (Br_2) posteriad to the anus. A third row began with the upper jaw photophore (Br_1) and ended with the upper opercular photophore. Fraser-Brunner proposed that the photophore patterns of all extant lanternfish species were derived by upward migration of certain photophores on the ventral and lateral rows of the ancestral form. His chief evidence for such upward migration was that, in present-day myctophids, certain lateral photophores, such as the posterior two SAO and the POL, lie above gaps in the ventral series. These gaps were presumably produced by the upward migration of photophores to the lateral position they now occupy. He found other indirect evidence in the presence of small modified scales which overlie certain of the lateral photophores in some species. Since these scales were out of the meristic lines of the larger scales, Fraser-Brunner concluded that they were scales that had been "taken with" the photophores during their upward migration.

Fraser-Brunner's (1949) hypothesis has remained unchallenged or at least tacitly accepted by workers up to the present; however, we believe that it contains a number of deficiencies which warrant an alternative theory for the evolution of the photophore pattern in lanternfishes. Firstly, we believe that the presence of certain lateral photophores above gaps in the ventral row is tenuous indirect evidence of migration, since there are many examples of lateral photophores lying directly above photophores in the ventral series, and there are equally numerous examples of gaps in the ventral series with no overlying photophores whatsoever. Further, we find the presence of small specialized scales over certain of the lateral photophores to be inconclusive evidence of upward migration from the ventral series, since some lateral photophores are overlain by normal-sized scales that are aligned with the other scales in their row. Also, if a photophore had carried its scale with it dur-

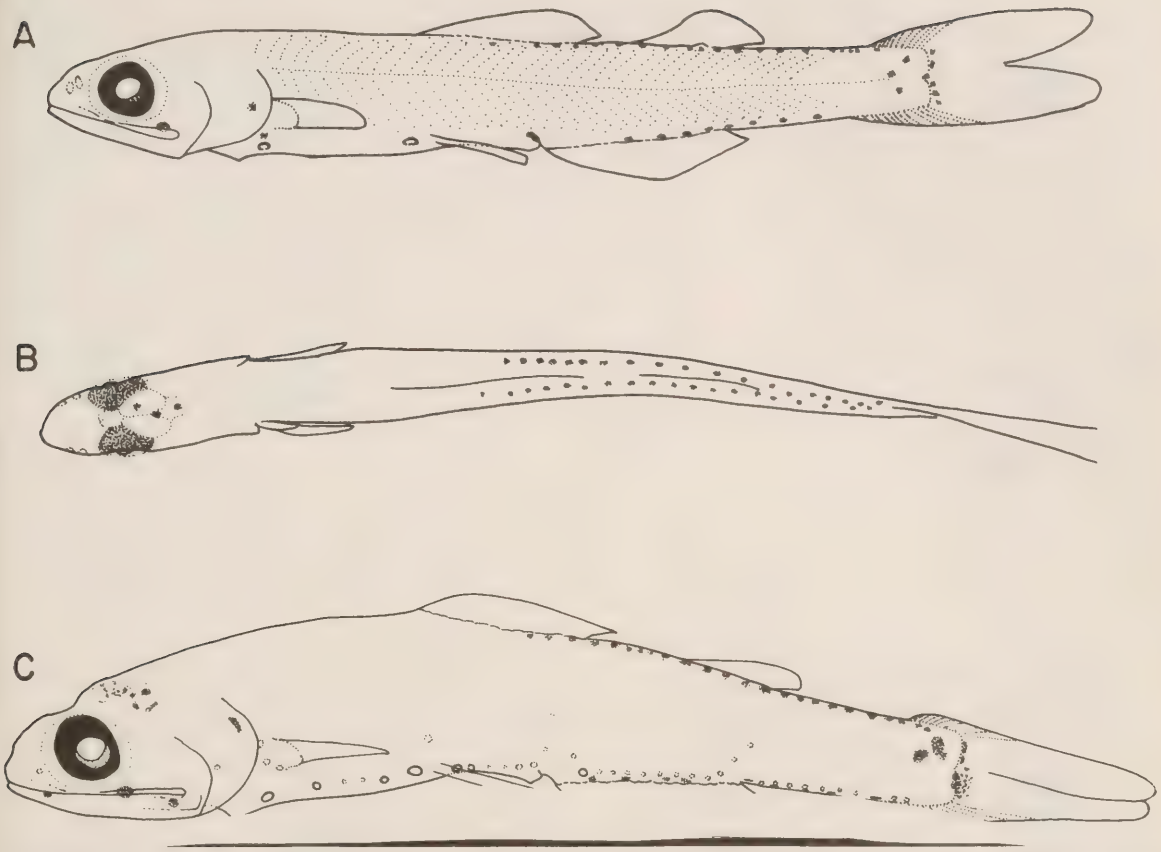

FIGURE 12.—Developmental stages of *Gymnoscopelus aphya* Günther.—A, 23.5-mm larva, U.S. NS *Eltanin* Station 319; B, 23.5-mm larva, dorsal view; C, 27.7-mm transformation stage, U.S. NS *Eltanin* Station 1341.

ing its upward migration, one might expect a comparable deletion or modification at its origin in the ventral scale row. There is none. Another major deficiency in the theory is its inability to explain the photophore pattern of a species such as *Notolychnus valdiviae* which has four pairs of photophores near the dorsal midline. If derived from the ventral series, the dorsal photophores would be supplied by peripheral nerves of the ventral or medial spinal rami that would have to extend dorsad across the horizontal septum; such an arrangement seemed so unlikely for species with photophores above the lateral line that we traced the nerve supply to such photophores in *Triphoturus mexicanus*, *Bolinichthys* sp., and *Notolynchnus valdiviae*. In *T. mexicanus* the VLO, SAO_3, POL_2, and Prc_3 lie above the lateral line, and in *Bolinichthys* the latter three photophores lie above the line. These light organs are supplied by a branch of the lateral vagus nerve, the superficial lateral-line nerve. In *Notolychnus* the VLO, SAO_3, POL_2 and Prc_2 lie extremely high on the body near the dorsal midline. The VLO and SAO_3 are supplied by the dorsal ramus of the lateral vagus nerve. The nerve supply to the POL_2 was difficult to determine but appeared also to be the dorsal ramus of the lateral vagus nerve. The Prc_2 is innervated by the superficial lateral-line nerve.

Ray (1950), in her detailed study of the peripheral nervous system of *Stenobrachius leucopsarus*, showed that all body photophores, except three pairs, are supplied by ventral rami of spinal nerves. The exceptions, SAO_3, POL, and Prc_4,

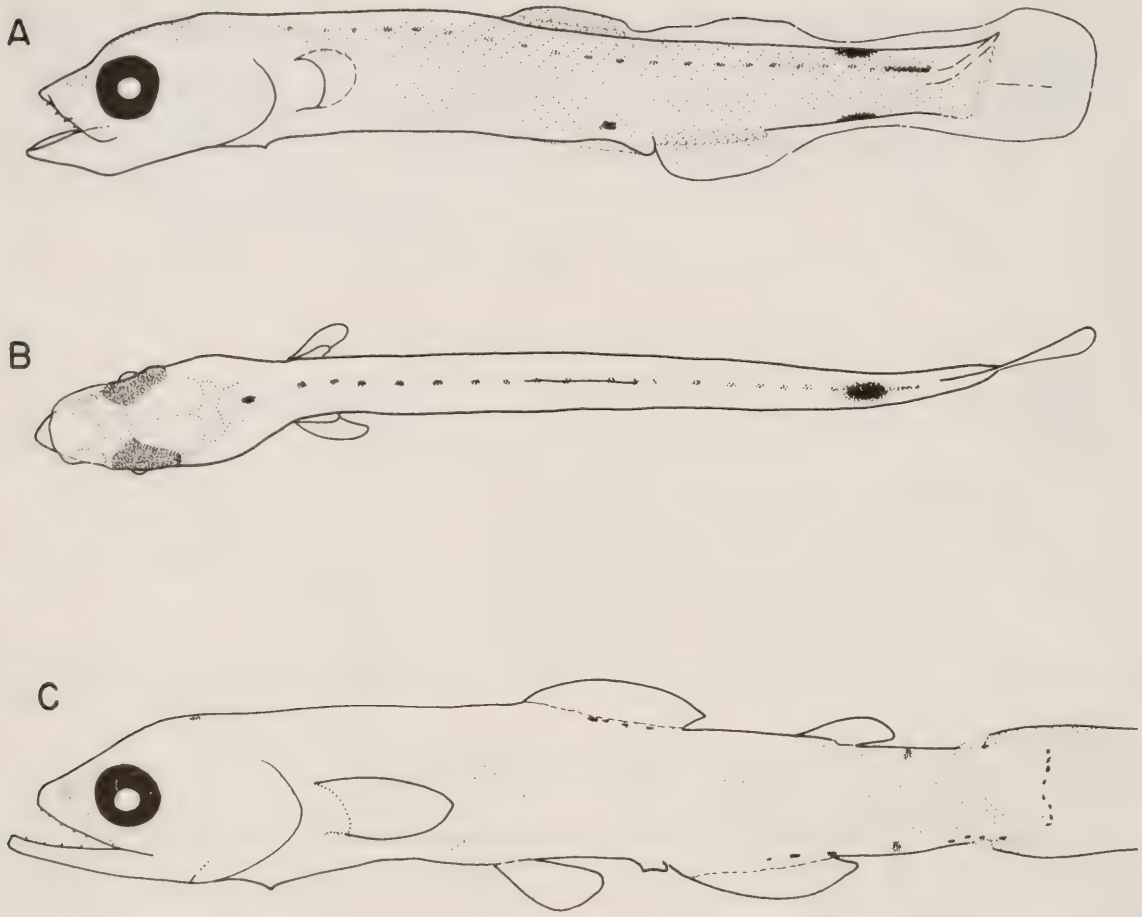

FIGURE 13.—Developmental stage of *Taaningichthys minimus* Tåning.—A, 7.3-mm larva, Hawaii Institute of Marine Biology, China Hat Series 3; B, 7.3-mm larva, dorsal view; C, 14.4-mm larva, SIO-FCRG Cruise 71-2.

are innervated by medial rami of spinal nerves; however, the first two of these each receive a small ramulus from a ventral spinal ramus. Ray believed that the innervation of lateral body photophores by ventral components of spinal nerves supported Bolin's (1939, p. 131-132) suggestion that lateral body photophores were derived by upward displacement of certain photophores from a single pair of ventral photophore rows. In lanternfish, such as *T. mexicanus*, *Bolinichthys*, and *Notolychnus*, the photophores which lie above the lateral line have always been considered homologous to their counterparts that lie below the line in other genera. Our finding of a cranial nerve supply for photophores above the lateral line in *T. mexicanus*, *Bolinichthys* sp., and *Notolychnus* casts considerable doubt on the theory that these photophores could have arisen from upward displacement, "from a primitively ventral and strictly linear series" (Bolin, 1939, p. 131-132) or even from "two ventrally located, parallel series of photophores, such as we find in *Vinciguerria*" (Bolin, 1939, p. 97).

An alternative hypothesis for the evolution of photophore patterns became apparent to us when studying the transforming stages of *Scopelopsis* (Figures 2, 3). It is obvious that in these specimens, the so-called primary photophores

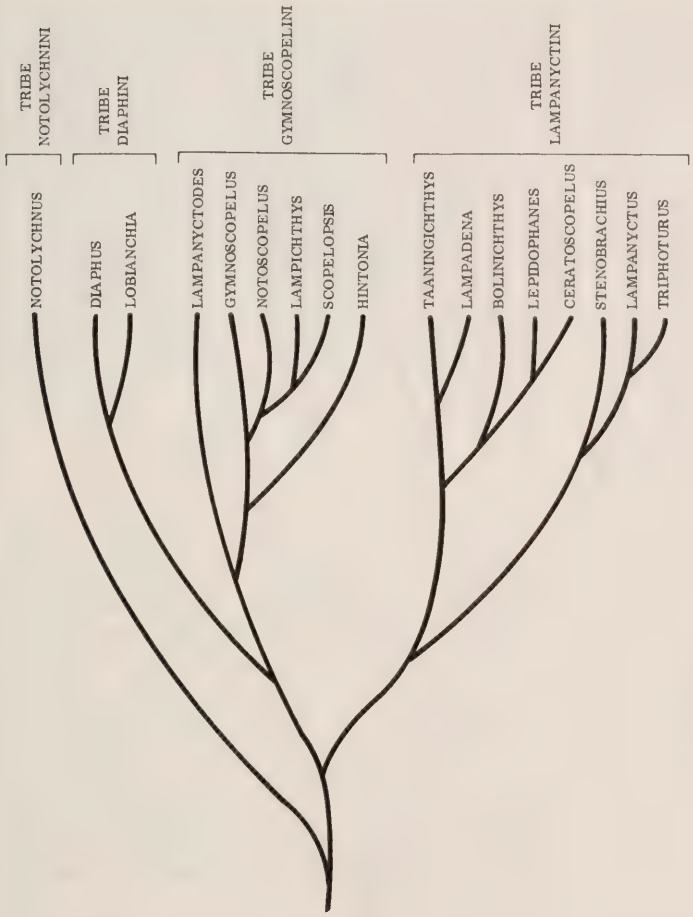

FIGURE 14.—Dendrogram of Paxton's (1968, 1972) arrangement of genera and tribes in the subfamily Lampanyctinae.

take their places very properly in the horizontal lines of smaller secondary photophores that cover the body. In these remarkable specimens, the primary photophores appear merely as enlarged members in the meristic series of light organs. Accordingly, it is tempting to speculate that this reflects a possible ancestral stage in the evolution of myctophid photophore patterns. We postulate that the archetypal pattern of light organs in lanternfishes was a generalized arrangement consisting of a single unspecialized photophore at the posterior margin of each scale pocket and a series of similar photophores distributed over the head. The progressive enlargement and specialization of certain photophores of the generalized pattern and concurrent diminution or loss of the "secondary" photophores would seem a propitious mechanism for adaptation and subsequent species diversification. The enlargement of photophores in the ventral midline to form a pair of longitudinal rows was universal in the family. Clarke (1963) suggested that these downward oriented photophores emit a continuous light of ambient wavelength which conceals the fish by breaking up its silhouette, that would otherwise be easily detected by predators hunting from below. This and other theories for the universality of the ventral photophore rows are discussed by McAllister (1967). The placement of the ventral and lateral photophores in a pattern unique to each species is an obvious mechanism for species recognition and reproductive isolation (Harvey, 1952, 1957; Marshall, 1954; Bolin, 1961).

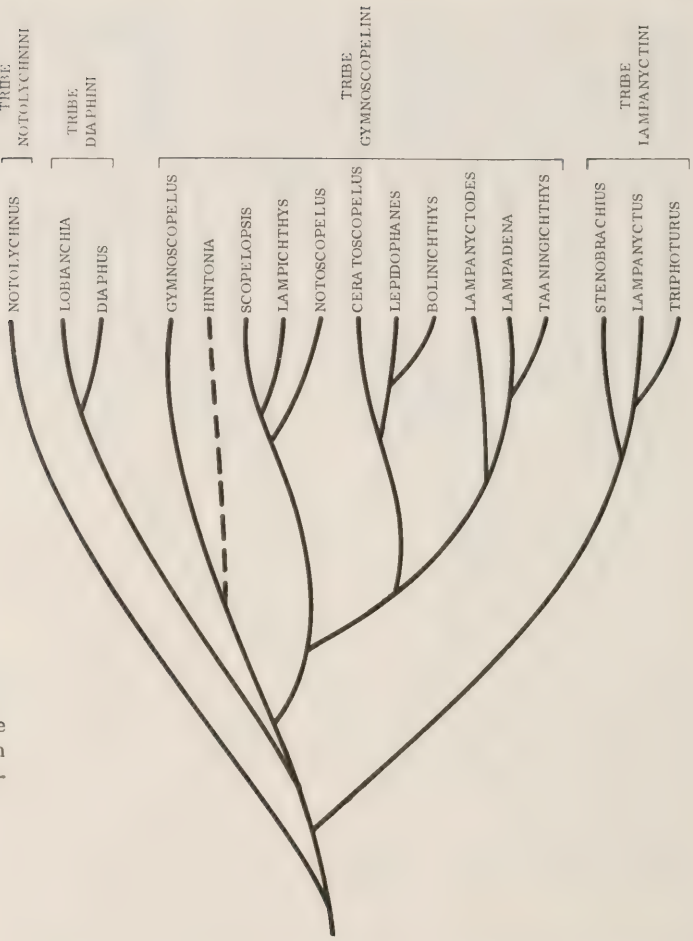

FIGURE 15.—Dendrogram showing the generic relationships and tribal division of the subfamily Lampanyctinae as suggested by larval characters.

Whatever were the adaptive forces that marshalled the light organs of myctophids into specific patterns, we believe that the ancestral myctophids had unspecialized photophores distributed over the head and body (one at the margin of each scale pocket) and that the specific patterns were derived by enhancement of some photophores and the concomitant deletion of others. Among the 28 known genera of myctophids are six (*Scopelopsis, Hintonia, Lampichthys, Bolinichthys, Lepidophanes,* and *Lampanyctus*) in which at least some species have minute photophores on the body, in addition to the typical pattern of primary photophores. The minute photophores may occur at every scale pocket (e.g., *Scopelopsis*) or may be restricted to a certain region of the body (e.g., *Hintonia*). Typically, those species with such minute photophores also have one or more head photophores that are lacking in most other myctophids. Previous workers have considered the minute photophores of these genera to be secondary structures, which have evolved after the primary organs; however, we believe that they reflect an ancestral stage in the evolution of photophore pattern. We believe that *Scopelopsis* most closely approximates the photophore pattern of ancestral myctophids since the distinction between "primary" and "secondary" organs is less apparent than in the other genera retaining secondary photophores. Moreover, every photophore position described for lanternfishes has its counterpart in *Scopelopsis*, and we find that every known myctophid photophore pattern can be generated

by enhancement of selected photophores of this species. Such a mechanism for the evolution of photophore pattern seems much less cumbersome than the theory of upward migration of photophores from the ventral series. The minor upward displacement of some ventral photophores may be a plausible explanation for the slightly arched AO and VO rows found in some myctophids but, for reasons outlined above, we find it improbable that such a mechanism could be responsible for the profoundly diverse photophore patterns of contemporary lanternfishes.

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THE FISH FAMILY MORIDAE IN THE EASTERN NORTH PACIFIC WITH NOTES ON MORID OTOLITHS, CAUDAL SKELETONS, AND THE FOSSIL RECORD

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ABSTRACT

Four species of morids (*Antimora microlepis, Microlepidium verecundum, Physiculus nematopus,* and *P. rastrelliger*) are known to inhabit waters of the eastern North Pacific. These can be differentiated by numerous external and internal characters including finray counts, dentition, head shape, gill-raker counts, vertebral counts, and otoliths. *Microlepidium grandiceps* and *Physiculus longipes* were found to be junior synonyms of *M. verecundum* and *P. nematopus,* respectively.

Only three characters appear to be infallible for recognizing members of family Moridae: large fontanelles in the exoccipitals through which elongate hornlike projections of the swimbladder extend and contact the auditory capsules; the otoliths; and the caudal skeleton. Otoliths and the caudal skeleton were used in evaluating the fossil record, and none of the 10 species that have been accepted as being morids, but which were known only from skeletal imprints, could be proven to be correctly identified. On the other hand, four species known only from fossil otoliths are unquestionably morids.

Morid otoliths are so distinctive and so characteristic that they appear to be reliable for distinguishing many species and most, if not all, genera. Based upon an examination of sagittal otoliths from 15 morid genera it was possible to distinguish four natural groups. These were designated the *Mora*-group containing *Mora, Halargyreus, Antimora,* and *Lepidion*; the *Physiculus*-group containing *Physiculus, Gadella, Tripterophycis, Brosmiculus, Laemonema,* and *Microlepidium*; the *Pseudophycis*-group containing *Pseudophycis, Auchenoceros, Lotella,* and *Salilota;* and the *Actuariolum*-group containing *Actuariolum,* a genus known at present from two species of extinct Miocene morids and one species living in the Antarctic.

The capture of a juvenile *Physiculus rastrelliger* off Eureka and the finding of their otoliths in a Pliocene deposit near the southern shore of Humboldt Bay aroused the curiosity of one of us (Barker) regarding the past and present distribution of this small morid. Every avenue we investigated led to frustration in the form of erroneous or unreliable information that had been perpetuated and compounded through the years. What appeared to be a 1- or 2-day project became a major undertaking just to satisfy a mild curiosity.

Unfortunately, before he was able to do much more than lay the groundwork for this study, Lloyd Barker lost his life at sea while acting as an official observer for the California Department of Fish and Game on a sea lion catching boat that sank near Santa Rosa Island. Although many of the problems were discussed prior to Lloyd Barker's death, all errors, omissions, and oversights are the sole responsibility of the senior author.

Morids generally were unrecognized and unaccepted at the family level until Svetovidov (1948) pointed out for the third time the uniqueness of the swim bladder connection with the auditory capsule, a character that was infallible for distinguishing morids from other gadoids. In a subsequent study, Svetovidov (1967) distinguished additional morid genera and further

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established the validity of the "swim bladder and fontanelle" character, while other workers publicized equally stable characters in the morid caudal complex (Rosen and Patterson, 1969) and the sagittal otoliths (Schmidt, 1968; Karrer, 1971).

In spite of such common knowledge, the validity of characters used for distinguishing genera has not been demonstrated, and any estimate of speciation would be wild at best. Perusal of available literature indicates that perhaps 20 morid genera are recognized from among the 25 or so available names. Since about half of these genera are monospecific, it seems highly probable that a critical study would result in a substantial reduction.

We limited our research to those morids inhabiting the eastern North Pacific for three reasons: (i) it is the faunal region of greatest immediate concern to West Coast fishery biologists and ichthyologists, (ii) study material was readily available, and (iii) the problems appeared to be solvable in the time we were able to budget for the study. Our work with morid otoliths and the fossil record stems from a long-seated interest in these two subjects, and knowledge of the otoliths and the caudal complex was needed in order to interpret the fossil record.

KEY TO GENERA AND SPECIES OF MORIDAE IN THE EASTERN NORTH PACIFIC

1. Snout projecting well beyond mouth as a flat, pointed rostrum; first ray of first dorsal filamentous, longer than head; 57 to 58 vertebrae; 36 to 38 caudal rays; a small oval patch of teeth on head of vomer ..... *Antimora microlepis*

   Mouth terminal, snout not flattened nor projecting; first ray of first dorsal not produced, equal to less than one-half head length; 43 or fewer vertebrae; 32 or fewer caudal rays; vomerine teeth absent or forming a single row, never in clumps or patches 2

2. Pelvic rays 2; vomerine teeth in a single row across head of vomer; 39 to 42 rays in second dorsal; 39 to 42 rays in anal; 44 to 46 vertebrae; no black fossa (luminous area) on belly between and behind pelvic fin bases ..... *Microlepidium verecundum*

   Pelvic rays 6 or 7; no teeth on vomer; 52 to 67 rays in second dorsal; 56 to 67 rays in anal; 52 to 55 vertebrae; a black fossa on midline of belly behind pelvic fin bases 3

3. Pelvic rays 6; gill rakers 16 to 19, 12 to 14 on lower limb; caudal rays 22 to 25; black fossa on belly round, width equal to length or nearly so; chin and throat densely scaled, rough to touch ..... *Physiculus nematopus*

   Pelvic rays 7; gill rakers 26 to 30, 18 to 22 on lower limb; caudal rays 27 to 32; black fossa on belly over twice as long as wide; chin and throat naked or with a few embedded scales, smooth to touch ..... *Physiculus rastrelliger*

SPECIES ACCOUNTS

Antimora microlepis Bean, 1890

D. 4(4-5),[3] 50(50-55)[3]; A. 37(39-42)[3]; C. 37; P. 20; P_2. 6(6-7)[3]; Br. 7; rakers on first gill arch 5 + 15 = 20; posterior rakers on first gill arch 3 + 12 = 15; vertebrae including hypural 24-25 + 33 = 57-58.

There is a small round patch of teeth on the head of the vomer; those in the jaws are villiform and in several rows. The broad depressed snout forms a spadelike rostrum with sharp lateral margins. The mouth is inferior. The elongate barbel at the tip of the lower jaw is conspicuous. The filamentous first ray of the first dorsal fin is more than twice as long as the next longest ray. The second dorsal and anal fins are deeply indented posteriorly and terminate adjacent to the ninth from last vertebra, including the hypural. The caudal rays com-

[3] Counts in parentheses are from Clemens and Wilby (1961).

mence adjacent to the sixth from last vertebra.

Schroeder (1940) reported that *A. viola, A. microlepis,* and *A. rhina* are synonyms of *A. rostrata* (Günther, 1878), and Clemens and Wilby (1961) and Fitch and Lavenberg (1968) followed this decision in reporting *Antimora* from the eastern North Pacific. Unfortunately, few of the characters used by Schroeder to support his action are of value for combining (or distinguishing) taxa at the species level. Type localities for *A. rostrata, A. viola, A. microlepis,* and *A. rhina* are the Indian Ocean, the western Atlantic, off Queen Charlotte Island, and off Panama, respectively. In view of the great distances separating these type localities, and until material from all four areas can be examined critically and compared in minute detail, we prefer to retain *microlepis* for the *Antimora* found in the eastern North Pacific.

A. microlepis has been reported as ranging from Central America (Fitch and Lavenberg, 1968) to Misaki, Japan (Svetovidov, 1948), but we have not seen material from south of Mazatlán, Mexico, or from west of the Bering Sea. Although we examined more than 50 individuals from the eastern North Pacific for key characters, we recorded meristic data on only one, a small specimen (LACM[4] 30400-2) trawled near San Clemente Island, Calif.

Microlepidium verecundum (Jordan and Cramer, 1897)

D. 7-9, 39-42; A. 39-42; C. 29-32; P. 19-22; P_2. 2; Br. 7; rakers on first gill-arch 5-6 + 11-13 = 17-19; posterior rakers on first gill-arch 3 + 11-12 = 14-15; vertebrae including hypural 11-12 + 33-34 = 44-46.

About seven teeth in a single row form a gently curved bow on each side of the head of the vomer. The lower jaw contains a single row of conical, sharply pointed teeth; in the upper jaw, there are two rows of teeth near the center and three irregular rows along the sides; all jaw teeth are similar in size and shape. A barbel is present at the tip of the lower jaw, but this is so tiny and inconspicuous it often can be located only with the aid of a microscope. The dorsal and anal fins terminate adjacent to the eighth from last vertebra, including the hypural; the caudal rays commence adjacent to the fifth from last vertebra.

[4] Institutions containing specimens studied are listed with standard abbreviations in Acknowledgments.

TABLE 1.—Proportional measurements for three species of morids found in the eastern north Pacific.

Measurement[1]	*Microlepidium verecundum*	*Physiculus nematopus*	*Physiculus rastrelliger*
Standard length	51-101	93-158	79-207
Total length	1105-1126	1080-1120	1079-1124
Head length	267-283	245-285	242-290
Snout length	049-058	057-073	062-076
Maxillary length	116-125	114-136	117-136
Diameter of fleshy orbit	082-093	062-079	067-081
Longest gillraker length	025-034	018-027	018-028
Snout to first dorsal fin insertion	274-300	253-288	262-298
Snout to anal fin insertion	390-426	317-351	316-359
Snout to pectoral fin insertion	268-287	249-288	253-292
Snout to pelvic fin insertion	191-247	213-246	200-255
Pectoral fin length	208-238	161-179	143-185
Pelvic fin length	244-292	272-298	122-169
Longest ray in first dorsal fin	085-108	102-123	098-127
Longest ray in second dorsal fin	094-115	092-112	078-107
Longest ray in anal fin	099-116	092-112	077-107
Caudal peduncle depth	016-019	020-025	018-022
Peduncle length (dorsal)	108-117	048-061	069-095
Peduncle length (ventral)	108-117	048-061	069-095
Number of specimens	10	10	20

[1] Standard lengths are in millimeters; all other measurements expressed as thousandths of standard length.

Morphometric data are presented in Table 1.

The unique holotype, described as *Lepidion verecundum,* was trawled at *Albatross* station 2993 (lat 18°17'15"N, long 114°44'30"W) near Clarion Island in 665 m (364 fm); it was reported as being a "young specimen, 2¼ inches long." Subsequently, Garman (1899) noted that in a specimen "only three and one-half inches in length, its ovaries are filled with eggs that appear to be about mature." We examined a female 83.5 mm SL that was running ripe in January and have seen females as small as 67 mm SL with developing eggs in their ovaries. The largest specimen we have seen was 101 mm SL (112 mm TL).

M. verecundum has been captured throughout the oceanic area from just south of Cape San Lucas, Baja California (lat 22°45'N), to about 322 km SW of Pta. San Telmo (lat 15°57'N) and offshore to Clarion Island (lat 114°44'30"W). Within this area they have been taken with midwater trawls fished well beneath the surface, and

their remains have been found in the stomachs of deep-feeding predators.

In describing *Lepidion verecundum*, Jordan and Cramer (1897) reported "dorsal VIII-40; anal 37; ventral apparently 1 (some rays broken on each side)." A radiograph of the 51-mm-SL holotype (USNM 47748) revealed that these counts should be D. 8, 39; A. 40; P_2. 2; in addition there are 19 pectoral rays, 30 caudal rays, 7 branchiostegals, and 45 vertebrae of which 12 are precaudals.

In describing the genus *Microlepidium*, Garman (1899) made several erroneous observations on the specimens he examined. He reported a "V-shaped single series of teeth on the vomer" (the single series is slightly bowed or crescent-shaped), ventral fins comprised of four rays (there are only two), and no barbel (a barbel is present, though microscopic). He noted that his *M. grandiceps* could be "distinguished from *M. verecundum* Gilb. [sic] by the larger number of rays and the shallower notch in the anal fin, the greater length of ventrals, pectorals and maxillary, and the larger number of scales in a longitudinal series." His report of "A. 4" for *M. grandiceps* is obviously a typographical error, and since the radiograph of the holotype of *Lepidion* [=*Microlepidium*] *verecundum* showed 40 anal rays, this character is negated for distinguishing the two. The other characters Garman used for separating *M. grandiceps* from *M. verecundum* are equally without basis in fact, and since we were unable to find even slight variance between the two, we relegate *M. grandiceps* to the synonymy of *M. verecundum*.

We have examined material of *M. verecundum* from the following localities, all off Mexico; lat 22°51′30″N, long 108°14′W, 12 Nov. 1967, *Velero* 11750, 1 spec.; lat 22°45.2′N, long 110°00.7′W, 16 Jan. 1969, *Alaska* 69A1-11, 2 specs.; lat 21° 13.8′N, long 107°08′W, 18 June 1952, SIO66-411, 1 spec.; lat 20°56.2′N, long 108°44′W, 16 May 1960, SIO63-979, 1 spec.; lat 20°21′N, long 106° 10′W, 19 Jan. 1970, *Velero* 13759, 3 specs.; lat 20°16′N, long 111°32.2′W, 19 Apr. 1954, SIO54-88, 7 specs.; lat 19°54.1′N, long 108°38.9′W, 18 May 1960, SIO63-981, 3 specs.; lat 19°52′N, long 113°20.5′W, 21 Apr. 1954, SIO54-92, 13 specs.; lat 18°41′N, long 111°00′W, 20-21 Apr. 1954, SIO54-91, 26 specs.; lat 18°41′N, long 110°51′W, 18 Feb. 1971, *Searcher* 57, LACM 31751-3, 1 spec.; lat 18°17′15″N, long 114°44′30″W, 6 Mar. 1889, *Albatross* 2993 (x-ray of holotype examined); lat 15°57′N, long 105°56′W, May 1968, remains of 16 fish including otoliths in stomachs of *Dosidicus gigas*.

Physiculus nematopus Gilbert, 1890

D. 9-11, 57-67; A. 62-67; C. 22-25; P. 23-25; P_2. 6; Br. 7; rakers on first gill-arch 4-6 + 12-14 = 16-19; posterior rakers on first gill-arch 3-5 + 10-13 = 14-17; vertebrae including hypural 13-14 + 38-40 = 52-53.

There are no teeth on the vomer and palatines; those in the jaws are villiform and in bands. A round block fossa, reportedly a luminous organ, lies on the midline of the belly about opposite the posteriormost base of the pelvic fins. The chin and throat region are densely scaled and rough to the touch. The dorsal and anal fins terminate adjacent to the sixth from last vertebra, including the hypural; the caudal rays commence adjacent to the fourth from last vertebra.

Morphometric data are presented in Table 1.

Jordan and Evermann (1898) designated specimens labeled USNM 46486 and 46555 as lectotypes from among the material collected in the Gulf of California by the *Albatross*. *P. nematopus* ranges from the northern Gulf of California (lat 30°26.3′N) to the Gulf of Panama (lat 07° 06′15″N) and has been captured at depths ranging from 76 to 1,271 m. Specimens from depths greater than about 366 m probably are captured well off the bottom; juveniles particularly are often taken in or near the scattering layer. The largest individual we have seen was 170 mm SL (189 mm TL).

Although *P. nematopus* was described from material dredged in the Gulf of California north of La Paz (*Albatross* stations 2997, 3011, 3015, and 3016), Goode and Bean (1895) in recording the species noted that it was found "off the southern coast of California." This erroneous statement has been perpetuated in the literature ever since (Jordan and Evermann, 1898; Jordan, Evermann, and Clark, 1930).

Garman (1899) described *P. longipes* from Panama and noted that it can be "distinguished from *Phyciculus* [*sic*] *nematopus* Gilb., by a greater number of rays in the dorsal and a smaller number in the ventrals," but the dorsal and ventral ray counts that he gave for *P. longipes* (D.10 + 55-63; V.6) are identical to counts we made on *P. nematopus*. We examined a radiograph of one of Garman's types of *P. longipes* (USNM 57876) and were unable to find any character to distinguish it from *P. nematopus*. We therefore relegate *P. longipes* into the synonymy of *P. nematopus*.

We examined material from the following localities: **Gulf of California:** 18.5 km SE of San Felipe, Feb. 1949, UCLA W49-91, 1 spec.; lat 30°26.3′N, long 114°12.1′W, 19 Jan. 1968, 76-86 m, SIO68-92, 20 specs.; lat 30°20′N, long 114°10′W, 19 Jan. 1968, 148-225 m, SIO68-93, 106 specs.; lat 29°54′N, long 113°03.2′W, 30 Mar. 1960, 110 m, SIO60-119, 6 specs.; lat 29° 19.9′N, long 113°10.4′W, 19 Jan. 1968, 265-283 m, SIO68-94, 90 specs.; lat 23°51′N, long 107°33′W, 137 m, SIO59-264, 1 spec.; lat 23° 50.5′N, long 107°18.2′W, 77-88 m, SIO59-263, 2 specs. **Costa Rica:** off Punta Quepos, Puntarenas, 16 July 1969, LACM 30721-3, 1 spec.; ±9 km off Cape Velas, 7 May 1963, UCLA W63-142, 3 specs.; near Puntarenas, UCR 490, 3 specs.; 18.5 km SW of Isla Canos, 143 m, 15 July 1969, UCR 328-6, 6 specs. **Panama:** USNM 57876, 1 spec., paratype of *P. longipes*.

Physiculus rastrelliger Gilbert, 1890

D. 8-11, 52-62; A. 56-63; C. 27-32; P. 24-28; P_2. 7; Br. 7; rakers on first gill-arch 7-9 + 18-22 = 26-30; posterior rakers on first gill-arch 4-6 + 14-20 = 18-24; vertebrae including hypural 12-14 + 40-42 = 52-55.

There are no teeth on the vomer and palatines; those in the jaws are villiform and in bands. An elongate black fossa, reportedly a luminous organ, lies on the midline of the belly about opposite the posteriormost base of the pelvic fins; it is two or three times as long as wide. The chin and throat region are naked, or at most a few scattered embedded scales are present. The dorsal and anal fins terminate adjacent to the eighth from last vertebra, including the hypural; the caudal rays commence adjacent to the fifth from last vertebra.

Morphometric data are presented in Table 1.

Jordan and Evermann (1898) designated the specimen labeled USNM 48266 as the lectotype, but did not give a locality of capture. Daniel M. Cohen (personal communication) informs us that USNM 48266 is a lot of seven specimens from *Albatross* station 3045 and that these and a single specimen (USNM 44281) from the same station are both labeled as types. *Albatross* station 3045 was at lat 26°24′N, long 113°49′W in 336.5 m (Townsend, 1901). Thus, the type locality is approximately southwest of Bahía de Ballenas, Baja California. *P. rastrelliger* ranges from 20.7 km WSW of the Mad River, Calif., (lat 40°55′N, long 124°22.5′W) to the Gulf of Panama (lat 07°12′20″N, long 80°55′W). It seldom has been captured shallower than 183 m or deeper than 366 m, but verified depths range from 128 to 523 m. The largest individual we have seen was 207 mm SL (225 mm TL).

P. rastrelliger was originally described from material dredged at *Albatross* stations 2987 and 3045, both off central Baja California. For some unknown reason, but probably an error of omission (e.g., Baja), Goode and Bean (1895), in recording this species, noted both of these stations as "off the southern coast of California." That erroneous statement very likely caused Jordan and Evermann (1898) to ascribe this species to southern California. Not until 1923 however, was *P. rastrelliger* reported from California based upon material actually taken there (Fowler, 1923). Reports subsequent to Fowler's (Ulrey, 1929; Jordan, Evermann, and Clark, 1930; Barnhart, 1936) could have been based upon any of the previous three, but probably did not involve additional Californian captures. The listing of *P. rastrelliger* by Fitch and Lavenberg (1968) was based upon numerous Californian captures of the species, not specified in detail.

We have examined material from the following localities: **California:** lat 40°55′N, long 124°22.5′W, 12 Nov. 1970, 143-146 m, *N. B. Scofield* 70S8-21, 1 spec; off Gaviota, Santa Barbara Co., 6 Aug. 1967, 263 m, SBMNH 00229, 1 spec.;

13.9 km NW of Cavern Point, Santa Cruz Isl., 23 Jan. 1961, 229 m, UCLA W61-48, 3 specs.; lat 33°58′N, long 118°43′W, 5 Aug. 1969, 320-323 m, *N. B. Scofield* 69S5-16, 2 specs.; lat 33° 57′N, long 118°39′W, 5 Aug. 1969, 283 m, *N. B. Scofield* 69S5-18, 1 spec.; lat 33°35.5′N, long 118°05.3′W, 18 Aug. 1970, 128-146 m, Oxy 70 8-18, 12 specs.; lat 33°34.2′N, long 118°04.8′W, 19 Sept. 1970, 274 m, Oxy 70 9-19, 7 specs.; lat 33°32.2′N, long 118°08′W, 27 Jan., 9 Apr., 29 Apr., and 27 Oct. 1971, 274 m, Oxy 71, 16 specs.; 6.8 km WSW of Del Mar, 12 Oct. 1950, 274 m, SIO50-249A, 6 specs.; La Jolla area, 16 and 18 Aug. 1916, Barnhart coll. D42 and D49, SIO67-138 and SIO64-287, probably the two specimens reported by Fowler (1923); 14.8 km W. of Point Loma, 21 Jan. 1965, 347.5 m, SIO65-9, 1 spec. **Baja California:** off Bahía San Quentin, 1 Apr. 1962, 183 m, SIO62-522, 3 specs.; lat 28°18.1′N, long 115°24.1′W, 247-265 m, SIO71-122; 3 specs.; lat 27°59′58″N, long 116°32′W, 20 Aug. 1967, midwater trawl, surface to 1,372 m, *Velero* 11634, LACM 30019-12, 1 spec.; lat 27°12.9′N, long 114°30.5′W, 21-22 June 1971, prawn trap 183-210 m, *Alaska* 71A5-10, 8 specs.; lat 26° 04.5′N, long 113°40′W, 2 Dec. 1960, 229-293 m, SIO60-466, 39 specs. **Gulf of California:** lat 28°19.3′N, long 112°08′W, 293-307 m, SIO68-103, 15 specs.; lat 23°07.8′N, long 109°21.3′W, 10-11 Jan. 1968, 252 m, SIO68-56, 1 spec. **Costa Rica:** vicinity of Cabo Blanco, 17-21 May 1970, 219 m, UCR 427-7, 2 specs.; off Puntarenas, UCR490, 2 specs. **Panama:** lat 07°12′20″N, long 80°55′W, 23 Feb. 1891, 333 m, *Albatross* 3355, USNM 57877, 1 spec. x-ray.

MORID OTOLITHS

Although morid otoliths were illustrated and described by Vaillant in 1888 and have been reported both in paleontological and ichthyological literature during the 20th century, Schmidt (1968) appears to have been the first to record in print their uniqueness at the family level. He illustrated sagittae from five Atlantic genera of morids and noted that "although the form of the otolith within this family is by no means uniform, it is so characteristic that one can speak of a morid type."

The characteristic which makes the morid sagitta so distinct is the deeply channeled bifurcate cauda (posterior portion of the sulcus, or groove, on the inner face of an otolith). Frost (1924) noted this character with the statement "In no other species that has passed through my hands is a double cauda to be seen," but he apparently had not seen sufficient comparative material to recognize it as being diagnostic of the family.

Karrer (1971), in an excellent treatise on morid otoliths, pointed out that the thin bladelike ridge (crista) which divides the deeply channeled cauda longitudinally is actually the posterior colliculum. She reported that the diversity of characteristics found on the morid otolith are sufficiently reliable as to permit identification of the various genera. Based upon an examination of otoliths from 13 genera (20 species), she established three natural groups of living morids: the *Mora*-group comprising *Mora, Halargyreus, Antimora,* and *Lepidion*; the *Physiculus*-group comprising *Physiculus, Gadella, Tripterophycis, Brosmiculus, Laemonema,* and *Salilota;* and the *Pseudophycis*-group comprising *Pseudophycis* and *Auchenoceros.* She hesitantly places *Lotella* with the *Physiculus*-group.

Our investigations involved otoliths from 12 genera (Figures 1 and 5), and even though we had no prior knowledge of Karrer's research, we had decided that morid otoliths fitted into the identical three groups that she described, but we added a fourth to include an Antarctic species and two New Zealand fossils. To illustrate these we had drawings prepared of *Mora pacifica, Physiculus rastrelliger,* and *Pseudophycis bachus* (Figures 2, 3, and 4), and photographed the Antarctic species and one of the fossils (Figure 5). We believe that *Lotella,* based upon the proportion of ostium length into cauda length in *L. callarias,* is more closely allied with *Pseudophycis* than with *Physiculus. Salilota* also appears to belong with the *Pseudophycis*-group.

Since morid otoliths are likely to be encountered in food habit studies, fossil deposits, and bottom sediments, and could be useful in a taxonomic revision of the family, we have construct-

ed a key for identifying to genus the sagittae we have seen. Although obviously incomplete, this key can be expanded when otolihs of the dozen or so other genera come to hand. A species-by-species discussion of these otoliths is also presented.

KEY TO OTOLITHS OF 12 MORID GENERA

1. Lower rim of cauda bowed out posteriorly creating an expanded chamber ventral to the posterior colliculum ..... (*Mora*-group) .. 2

   Lower rim of cauda straight or turned downward at tip, but never forming an expanded area posteriorly 5

2. Anterior end of sagitta greatly expanded dorsally 3

   Anterior end of sagitta not expanded dorsally; height of otolith at anterior end about the same as height at center 4

3. Ratio of otolith height into length 1:1.6 or 1:1.7 ..... *Mora*

   Ratio of otolith height into length 1:2.0 or 1:2.1 ..... *Halargyreus*

4. Ventral portion of otolith projecting beyond dorsal portion anteriorly; ventral canal of cauda only slightly expanded posteriorly ..... *Antimora*

   Dorsal portion of otolith equal in length to ventral portion anteriorly, or projecting somewhat beyond; ventral canal of cauda greatly expanded posteriorly .....*Lepidion*

5. Ostium (anterior part of sulcus) comprising approximately one-half of otolith length .... (*Pseudophycis*-group) 6

   Ostium comprising approximately one-third or less of otolith length 8

6. Anterior end of otolith greatly expanded dorsally ..... *Auchenoceros*

   Anterior end of otolith pointed 7

7. Dorsal rim of cauda longer than ventral rim; otolith knobby and greatly expanded in middle one-third ..... *Pseudophycis*

   Dorsal rim of cauda shorter than ventral rim; otolith relatively smooth middorsally, never expanded in central portion ..... *Lotella*

8. Dorsal rim of cauda about equal in length to ostium; about half as long as ventral rim .... (*Physiculus-group*) .. 9

   Dorsal rim of cauda about twice as long as ostium; more than eight-tenths as long as ventral rim ..... (*Actuariolum-group*) .. *Actuariolum*

9. Otolith with a thin shelflike blade projecting ventrally from posterior portion of inner face ..... *Microlepidium*

   No ventral projection on inner face of otolith 9

10. Otolith broadly rounded anteriorly; greatest height in anterior one-third of length *Laemonema*

    Otolith somewhat pointed anteriorly; greatest height in middle one-third ..... *Physiculus*
    Tripterophycis

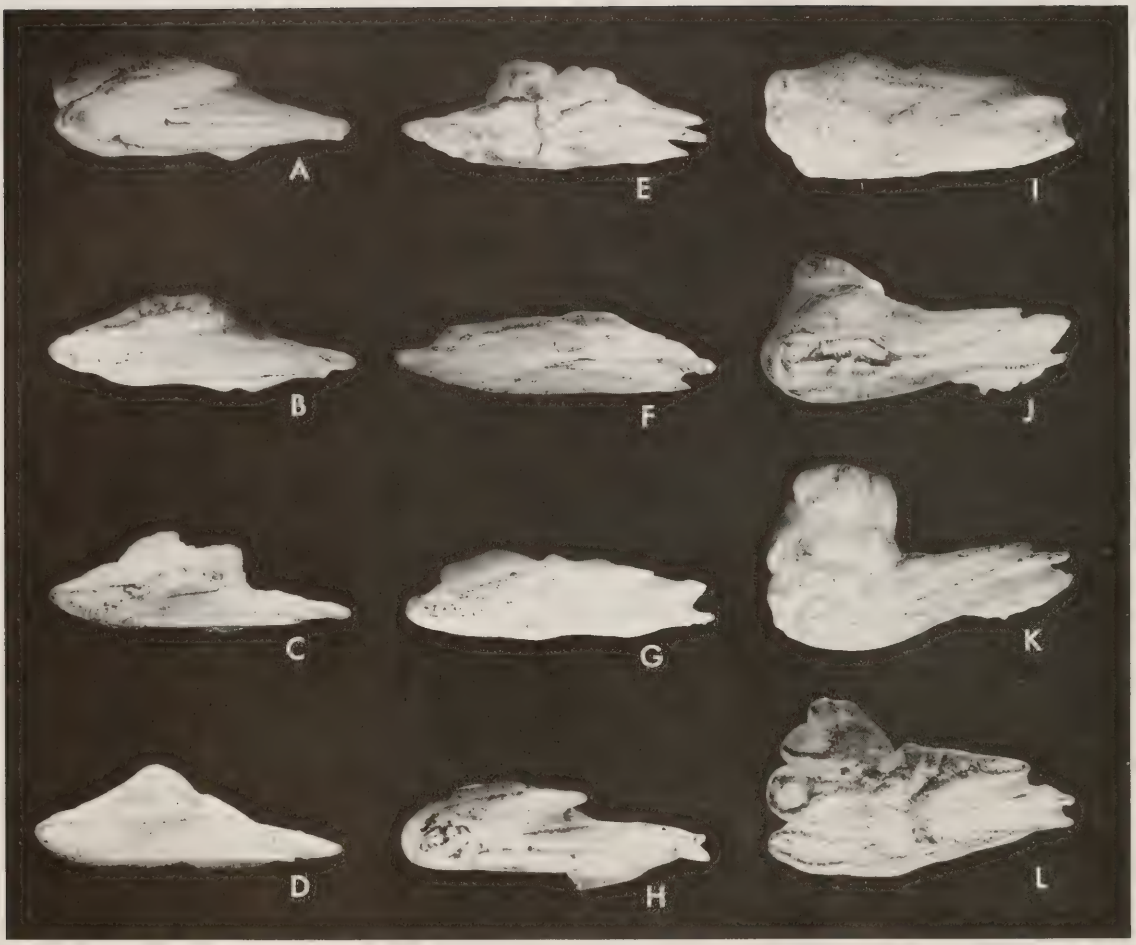

FIGURE 1.—Inner faces of right sagittae of 11 genera (12 species) of living morids: A. *Laemonema barbatulum*, B. *Tripterophycis gilchristi*, C. *Physiculus nematopus*, D. *Physiculus rastrelliger*, E. *Pseudophycis bachus*, F. *Lotella callarias*, G. *Antimora microlepis*, H. *Microlepidium verecundum*, I. *Lepidion eques*, J. *Halargyreus johnsonii*, K. *Mora pacifica*, L. *Auchenoceros punctatus*.

OTOLITH SPECIES ACCOUNTS

Mora-group (Figure 2)

Otoliths in this group are characterized by a bowing-out of the crista inferior (the ventral rim of the cauda or groove on the inner face of the sagitta), at about its midpoint, so that an expanded chamber is formed in the posterior portion of the lowermost canal. The crista superior (uppermost rim of the cauda) is more than three-fourths as long as the bladelike posterior colliculum (thin ridge which bisects the cauda horizontally). The anterior end of the sagitta may or may not be expanded dorsally. Sagittae of this group that have been illustrated are *Mora mora* (Vaillant, 1888, as *M. mediterranea;* Schmidt, 1968; Karrer, 1971); *Halargyreus johnsonii* (Fitch and Brownell, 1968, as morid #3; Schmidt, 1968, as *H. affinis;* Karrer, 1971), *Lepidion eques* (Schmidt, 1968; Karrer, 1971); and *Antimora rostrata* (Karrer, 1971).

FIGURE 2.—Drawing of right sagitta from *Mora pacifica* illustrating features of *Mora*-group otoliths.

Mora pacifica *Waite, 1914* (*Figure 1K*).—In the illustrated specimen (9.5 mm long) the ostium measures 3.8 mm and the cauda, 5.7 mm. The posteriormost 3.0 mm of the ventral canal is expanded. The sagitta of *M. pacifica* (11 pairs examined) differs consistently from that of *M. mora* (5 pairs examined) in the configuration, including angles, of the expanded anterior end. In all *Mora* otoliths examined, the ratio of height into length was 1:1.6 to 1:1.7.

Halargyreus johnsonii *Günther, 1862* (*Figure 1J*).—In the illustrated specimen (11.6 mm long) the ostium measures 4.5 mm and the cauda, 6.6 mm. The posteriormost 3.2 mm of the ventral canal is expanded. In the *Halargyreus* sagittae examined (5 pairs), the ratio of height into length was 1:1.20 to 1:1.21. This ratio is sufficient to distinguish *Halargyreus* otoliths from those of *Mora, Antimora,* and *Lepidion.*

Antimora microlepis *Bean, 1890* (*Figure 1G*).—In the illustrated otolith (10.4 mm long) the ostium is 3.9 mm long and the cauda, 5.9 mm. The posteriormost 3.5 mm of the ventral canal is expanded. The anterior ends of *Antimora* otoliths bulge very slightly dorsally, a characteristic which was grossly exaggerated in Karrer's (1971) illustration by inadvertently rotating the otolith out of lateral alignment. *Antimora* sagittae differ from those of *Lepidion* in that the anteroventral portion is somewhat pointed and extends well beyond the anterodorsal profile. They differ from those of *Mora* and *Halargyreus* in lacking the greatly expanded anterior end. More than 30 pairs of sagittae from *A. microlepis* were examined.

Lepidion eques (*Günther, 1887*) (*Figure 11*).—In the illustrated otolith (8.0 mm long), the ostium is 3.3 mm long and the cauda, 4.2 mm. The posteriormost 2.2 mm of the ventral canal is expanded. The anterior ends of *Lepidion* sagittae (4 pairs) are somewhat squared-off dorsally and project well beyond the anteroventral angle, a characteristic which distinguishes *Lepidion* otoliths from those of *Antimora.* The generally straight dorsal profile distinguishes this otolith from those of *Mora* and *Halargyreus.*

FIGURE 3.—Drawing of right sagitta from *Pseudophycis bachus* illustrating features of *Pseudophycis*-group otoliths.

Pseudophycis-group (Figure 3)

Otoliths in this group are characterized by having the ostium approximately equal in length to the cauda. The crista superior is more than three-fourths as long as the crista inferior. Greatest otolith height typically is at about mid-length, but in some (*Auchenoceros*) the anterior end is expanded (highest). Sagittae of this group that have been illustrated are *Pseudophycis bachus* (Frost, 1926, as *Physiculus bacchus;* Karrer, 1971, as *P. bacchus*), *P. barbatus* (Karrer, 1971), *P. breviusculus* (Karrer, 1971), *Lotella rhacina* (Karrer, 1971, as a member of the *Physiculus*-group), *Auchenoceros punctatus* (Karrer, 1971); and *Salilota australis* (Karrer, 1971).

Pseudophycis bachus (*Bloch and Schneider, 1801*) (*Figure 1E*).—In the illustrated otolith

(12.7 mm long), the ostium is 6.3 mm long and the cauda, 6.3 mm. In this genus, the crista superior is as long as or longer than the crista inferior, which distinguishes *Pseudophycis* sagittae from those of other genera in this group. An additional distinguishing character is the greatly expanded, knobby middorsal portion. Three pairs of *P. bachus* sagittae were available for examination.

Auchenoceros punctatus (*Hutton, 1873*) (*Figure 1L*).—In the illustrated otolith (4.7 mm long) the ostium is 2.3 mm long and the cauda, 2.4 mm. The greatly expanded anterior end easily distinguishes *Auchenoceros* sagittae from those of the other genera known to belong in this group. Two pairs of *Auchenoceros* otoliths were examined.

Lotella callarias *Günther, 1863* (*Figure 1F*).—In the illustrated otolith (11.3 mm long), the ostium is 5.7 mm long and the cauda, 5.5 mm. The combination of a pointed anterior end, a relatively smooth, unexpanded middorsal portion, and a crista superior that is shorter than the crista inferior distinguishes *Lotella* otoliths from those of other genera assigned to this group. Eight pairs of sagittae from *L. callarias* were examined.

Physiculus-group (Figure 4)

Otoliths in this group are characterized by having a relatively short ostium (comprising one-third or less of total otolith length) and a crista inferior that is almost twice as long as the crista superior. The anterior end of the sagitta usually is bluntly pointed but may be broadly rounded, it is never expanded. Sagittae of this group that have been illustrated are *Physiculus dalwigki* (Vaillant, 1888), *Physiculus peregrinus* (Kotthaus, 1970), *Physiculus capensis* (Karrer, 1971), *Physiculus* spp.? (Hatai, 1965, as *Odontobutis*; Fitch and Brownell, 1968, as morid #1 and morid #2), *Gadella maraldi* (Schmidt, 1968, as *Uraleptus maraldi*; Karrer, 1971), *Laemonema robustum* (Vaillant, 1888), *L. laureysi* (Schmidt, 1968; Karrer, 1971), *L. barbatulum* (Karrer, 1971), *Tripterophycis gilchristi* (Karrer, 1971), and *Brosmiculus imberbis* (Karrer, 1971).

FIGURE 4.—Drawing of right sagitta from *Physiculus rastrelliger* illustrating features of *Physiculus*-group otoliths.

Microlepidium verecundum (*Jordan and Cramer, 1897*) (*Figure 1H*).—In the illustrated otolith (3.5 mm long), the ostium is 0.8 mm long and the cauda, 2.7 mm. The crista superior (1.2 mm) comprises 33% of total otolith length and is slightly less than one-half the length of the crista inferior (2.3 mm). This otolith is characterized by having a thin ventrally directed "blade" projecting from the posteriormost 40% of the inner face. Ten pairs of sagittae from *M. verecundum* were examined.

Laemonema barbatulum *Goode and Bean, 1895* (*Figure 1A*).—In the illustrated otolith (7.3 mm long), the ostium is 2.4 mm long and the cauda, 4.6 mm. The crista superior (2.1 mm long) is slightly less than one-third the total otolith length, but more than one-half as long as the crista inferior (3.5 mm). Sagittae of *Laemonema* are broadly rounded anteriorly, and by this character can be distinguished from otoliths from other genera placed in the *Physiculus*-group. Eleven pairs of sagittae from *L. barbatulum* were examined.

Physiculus rastrelliger *Gilbert, 1890* (*Figure 1D*).—In the illustrated otolith (9.6 mm long), the ostium is 2.7 mm long and the cauda, 6.7 mm. The crista superior (2.7 mm long) comprises about 28% of total length and is slightly more than half as long as the crista inferior (4.8 mm). The otolith of *P. rastrelliger* can be distinguished from that of *P. nematopus* by the width of the

flattened area immediately above the crista superior. At any given otolith length, this area is only about half as wide on *P. nematopus* sagittae as on those of *P. rastrelliger*. We were unable to find any reliable character or set of characters for distinguishing *Tripterophycis* sagittae from those of *Physiculus*, but for any given species a careful comparison on a size-for-size basis appears to have merit. More than 30 pairs of sagittae from *P. rastrelliger* were examined.

Physiculus nematopus *Gilbert, 1890* (*Figure 1C*).—In the illustrated otolith (7.5 mm long), the ostium is 2.2 mm long and the cauda, 5.3 mm. The crista superior (2.2 mm long) comprises approximately 29% of total otolith length and is slightly more than half as long as the crista inferior. As in other species of *Physiculus*, the anterior end is almost conical in lateral outline. The lumpiness of the outer face is highly variable and is of no value for distinguishing species. Such lumps are always more pronounced on otoliths of juveniles than adults. Ten pairs of sagittae from *P. nematopus* were examined.

Tripterophycis gilchristi *Boulenger, 1902* (*Figure 1B*).—In the illustrated otolith (8.0 mm long), the ostium is 2.4 mm long and the cauda, 5.5 mm. The crista superior (2.2 mm long) comprises about 28% of total otolith length and very slightly exceeds half the length of the crista inferior (4.3 mm). Sagittae of *Tripterophycis* are very difficult to distinguish from those of other genera placed in the *Physiculus*-group that have conical anterior ends. Fifteen pairs of sagittae from *T. gilchristi* were examined.

Actuariolum-group (Figure 5)

Otoliths in this group are characterized by having a relatively short ostium (comprising one-third or less of total otolith length), a crista superior that is about three-fourths as long as the crista inferior, and an expanded anterior end. Sagittae which have been illustrated from this group are *A. bicaudatum* (Frost, 1924, as *Physiculus bicaudatus;* Karrer, 1971) and *A. terakohensis* (Frost, 1933, as *Physiculus terakohensis*; Karrer, 1971). Both of these species are extinct Miocene fossils from New Zealand.

Actuariolum *sp.* (*Figures 5A and 5B*).—Karrer (1971) errected the genus *Actuariolum* (type species *A. bicaudatum*) for Frost's (1924, 1933) two fossils, and in corresponding with one of us (Fitch) she thought that "one day a recent species will be found which will belong to this genus or show a very close relationship." Subsequently, in examining a number of unidentified morid otoliths from cruises of the *Eltanin*, we turned

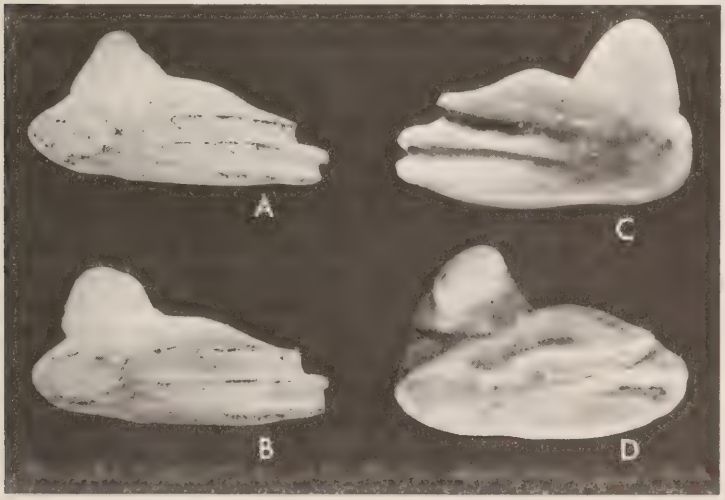

FIGURE 5.—Otoliths from *Actuariolum*: A and B, right sagittae, 5.2 and 4.2 mm long, respectively from an undescribed species collected at *Eltanin* station 1851, lat 49°40'S, long 178°53'E, 476-540 m, 3 Jan. 1967); C. and D., left and right sagittae from *A. terakohensis* collected in Lower Miocene deposits (Paratoetoe Fm.), Parengarenga Harbor, North Island, New Zealand, 2.9 and 3.0 mm long, respectively.

up several sagittae which match all salient characters of the fossil *Actuariolum*. In the illustrated specimens (from *Eltanin* station 1851, lat 49°40′S, long 178°53′E, 476-540 m) which are 5.2 and 4.2 mm long (Figures 5A and 5B) the ostium measures 1.7 and 1.2 mm; the crista superior, 2.9 and 2.6 mm; and the crista inferior, 3.3 and 2.9 mm, respectively.

For comparison, measurements of the illustrated fossil sagittae (*A. terakohensis* from the Paratoetoe Formation, Lower Miocene, Parengarenga Harbour, Figures 5C and 5D) are: total length, 2.9 and 3.0 mm; ostium, 0.9 and 1.0 mm; crista superior, 1.4 and 1.6 mm; and crista inferior, 1.9 and 1.9 mm, respectively.

Additional specimens of the undescribed species were trawled at *Eltanin* station 1411 at lat 51°00′S, long 162°01′E in 333 to 371 m. All morids from these two stations are in the U.S. National Museum fish collections (Hugh H. DeWitt, personal communication); those from station 1851 appear to represent an undescribed species.

THE MORID CAUDAL SKELETON

The morid caudal skeleton (Figure 6) not only is unique among gadoids, it is unique among teleosts. The two lowermost hypurals (1 and 2 of Rosen and Patterson, 1969) are fused at their base, which lies adjacent to the penultimate ural vertebra, but are otherwise autogenous. Above these, hypurals 3, 4, and 5 diverge posteriorly as separate entities from the ultimate ural vertebra. Among other gadoids, hypurals 1 and 2 are fused into a single plate, as are hypurals 3, 4, and 5.

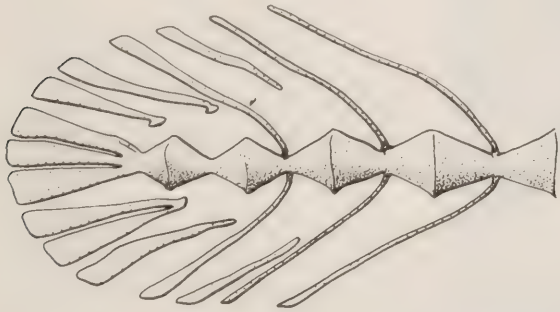

FIGURE 6.—Caudal skeleton of *Antimora microlepis*.

The remaining caudal skeleton, although typical for all morids examined, is not unique to family Moridae. Anterior to the dorsalmost hypural, there are successively: two autogenous epurals with bases adjacent to the penultimate ural vertebra, a neural spine arising from the first preural centrum, a free-floating splinter bone (dorsal accessory bone of Rosen and Patterson, 1969), and then neural spines on successive centra. Preceding the lowermost (first) hypural is an autogenous parhypural with its base adjacent to the penultimate ural centrum, a haemal spine affixed to the first preural vertebra, a free-floating ventral accessory bone, and then haemal spines on successive centra. The two epurals and the parhypural are present in most other gadoids, but the autogenous splinter bones (dorsal and ventral accessory bones) may or may not be present depending upon which gadoid genus is being examined.

Thus in any fossil skeletal imprint, if one could locate either the autogenous lowermost hypurals (1 and 2) with their fused base, or the diverging uppermost hypurals (3, 4, and 5) which project posteriorly from the ultimate ural centrum, the imprint unquestionably would be that of a morid.

FOSSIL MORIDS

The fossil record for family Moridae is based upon an abundance of skeletal imprints and otoliths, primarily from the Northern Hemisphere. Most of these were described prior to 1940, and most were placed in family Gadidae, which at that time included the morids. Danil'chenko (1953) was the first to assign fossil gadoids to family Moridae, but included *Melanonus* which Marshall (1965) subsequently removed to its its own family. In 1960, Danil'chenko suggested that *Eclipes* from the Californian Miocene was a morid, and at the same time he removed to family Brotulidae one of the species he considered a morid in 1953.

In our search for diagnostic characters which we could use to evaluate the fossil record, we found that only three features were infallible for distinguishing members of family Moridae:

the otoliths (Karrer, 1971), the caudal complex (Rosen and Patterson, 1969), and the large fontanelles in the exoccipitals through which elongate hornlike projections of the swim bladder extend and contact the auditory capsules (Svetovidov, 1948, 1967). Unfortunately, the diagnostic fontanelles cannot be distinguished in two-dimensional fossil imprints because of crushing, and three-dimensional skeletal remains are extremely rare, so one must rely upon either otoliths or the caudal complex to distinguish fossil morids.

Otoliths are abundant in most shelly marine deposits, but seldom are accompanied by other skeletal remains. On the other hand, in deposits where skeletal imprints abound, aragonitic substances, including otoliths, seldom remain. We know of only one deposit where otoliths have been found in situ in morid skeletal imprints. This is a Miocene diatomite deposit east of Los Angeles, Calif., and the morid is an undescribed species. Apparently several species examined by Danil'chenko (1960) from the Maikop deposits also have retained their otoliths, but he did not mention finding them in morids.

The tiny diagnostic hypurals of a morid caudal complex are difficult to observe unless the fossilized skeleton is preserved in lateral aspect, and such perfectly preserved specimens are extremely rare. In many of the gadoid skeletal imprints that we have seen, the caudal is either missing or so badly fragmented as to be virtually useless for determining relationships.

In commenting on the material reported upon by Danil'chenko (1953, 1960) we have relied heavily upon information obtained from Daniel M. Cohen, who examined much of it. During a trip to New Zealand, one of us (Fitch) examined fossil otoliths in the University of Auckland collections and noted sagittae from four species of Miocene morids, including both species reported upon by Frost (1924, 1933). In addition to two unreported species in the New Zealand Miocene, we have seen morid otoliths in the Miocene of California (two species), Jamaica (one species), and Poland (one species) which have not been reported in the literature. One of the two species from California probably represents an extinct genus, but additional comparative material will need to be examined before this can be determined for certain.

STRINSIA ALATA STEINDACHNER, 1859

Danil'chenko (1953) placed this species from the Upper Miocene of Europe in family Moridae, based upon its presumed resemblance to the recent *Strinsia tinca* Rafinesque, 1810, and to one of his fossils, *Strinsia sobievi*. Subsequently, he decided that his *Strinsia sobievi* was a brotulid (Danil'chenko, 1960), and Cohen and Torchio (1964) showed that Rafinesque's *Strinsia tinca* (the type species) was a macrourid. A search for Steindachner's *S. alata* in Vienna during April 1971 was unsuccessful (Daniel M. Cohen, personal communication). On the basis of published information it is not possible to associate *S. alata*, described from a poorly preserved partial skeletal imprint, with family Moridae.

ONOBROSMIUS ELONGATUS (KRAMBERGER, 1883)

Onobrosmius (type species *Brosmius elongatus* Kramberger, from the Upper Miocene of Croatia) was proposed by Bogachev (1938) for fossil cods with a single dorsal fin, which is separated from the caudal fin by a small interval. The absence of teeth on the vomer and palatines was weighted heavily by Danil'chenko (1960) in assigning *Onobrosmius* to family Moridae, but none of the characters he reported for this fossil genus or any of the species assigned to it is diagnostic for the family. It very likely is a gadoid, but its acceptance as a morid must await examination of material on which any of several diagnostic characters are clearly evident.

PHYSICULUS RASTRELLIGER GILBERT, 1890

Fitch (1969) reported finding otoliths from *P. rastrelliger* in Pliocene deposits at Los Angeles, San Pedro, and Newport Beach, Calif. In two of the three deposits that yielded *Physiculus* sagittae, they were the most abundant otoliths

present, representing 27 and 10% of the total otolith yield. Subsequently, Zinsmeister (1971) reported otoliths of *P. rastrelliger* from one of these same two deposits (LACM Invert. Paleo. Loc. 471) but did not give data on numerical abundance. One of us (Fitch) has found otoliths of *P. rastrelliger* in other southern Californian Pliocene and Pleistocene deposits at San Diego (LACM Invert. Paleo. Loc. 305), Newport Beach (Jamboree Blvd.), and near Rincon Point, Santa Barbara County (Bates Road), and a Centerville Beach locality (south Humboldt Bay) investigated by Barker also has yielded fair numbers. The Centerville Beach deposit appears to be of Pliocene age and represents the farthest north the species has been found.

ECLIPES VETERNUS JORDAN AND GILBERT, 1919

The type specimen of *E. veternus*, now in the California Academy of Sciences collection, is an incomplete (tail missing), poorly preserved skeletal imprint with the head rotated into a different alignment than the body. Jordan and Gilbert (1919) placed this small fish in family Apogonidae, but did not feel strongly regarding this assignment. Subsequently, Jordan (1921) moved it into family Gadidae, where it was retained by David (1943). Danil'chenko (1960), although he did not examine the type, felt that the genus *Eclipes* was much more closely related to family Moridae than Gadidae. However, the characters he used to support this opinion are not unique to the morids, either by themselves or in combination.

A careful examination of the type specimen revealed that not only is the type description wholly unreliable, there is no character or combination of characters that will permit assigning this small fish to any gadoid family. Only because of its small size, flattened anterior neural spines, and the shape, placement, and extent of its dorsal and anal fins can it be associated with other fossil gadoids in the Miocene diatomites and shales of California. Since *E. veternus* is the type species of *Eclipes*, but is not a morid, the name *Eclipes* is not available for use in family Moridae.

MERRIAMINA ECTENES JORDAN AND GILBERT, 1919

The identity of this little fish presents an enigma. In describing *M. ectenes*, Jordan and Gilbert (1919) placed it in family Brotulidae and designated specimen number XIII as the type. Their caption for Figure 1, Plate XXVII (Jordan and Gilbert, 1919) reads "*Merriamina ectenes* Jordan & Gilbert; type XIII (El Modena)," but the illustrated slab (Figure 1) clearly is labeled "XII."

In checking Jordan's fossils in the California Academy of Sciences collection we found their specimen XIV (Figure 3, Plate XXVII), which now bears in Lore David's handwriting the inscription "*Merriamina ectenis* [*sic*] type El Modena = *Eclipes veternus*," but we were unable to locate the type (XIII), the illustrated "type" (XII), or specimen CVII from which Jordan and Gilbert obtained their vertebral count. In the text (p. 56-57), they mentioned examining seven different specimens of *M. ectenes* and gave numbers for each of these, but "XII," the specimen illustrated as the type, is not listed, which leads us to believe that the use of "XIII" in the text and figure caption might have been a typographical error. In any event, the photograph of specimen XII (Figure 1, Plate XXVII) shows a poorly preserved gadoid-like fish with what is obviously a regenerated caudal fin. Thus, if specimen XII is in fact the type, *Merriamina ectenes* cannot be assigned to a family with any certainty, even though Jordan (1921) subsequently declared *M. ectenes* a synonym of *Eclipes veternus* and placed it in family Gadidae.

Jordan and Gilbert's other illustrated specimen (XIV), part of the type series, has hypural elements 3, 4, and 5 fused into a single plate, so it cannot be a morid (E. H. Ahlstrom, personal communication).

ECLIPES MANNI JORDAN, 1921

An examination of the caudal complex on Jordan's type specimen (No. 543), now in the California Academy of Sciences collection, revealed that hypurals 3, 4, and 5 are fused into

a single plate. For this reason, *E. manni* can not be assigned to family Moridae.

Although Jordan (1921) reported that the beautifully preserved type is "17½ inches long," and David (1943) lists it as being "355 + 35 = 390 mm [15½ inches] in length," we found that it measures only 339 mm SL (13⅜ inches), or 378 mm TL (14⅞ inches). David's measurement can be duplicated by including the lower jaw and by failing to note where the caudal rays actually terminate. Unfortunately, the lower jaw became disarticulated and moved forward during fossilization, so it cannot be used as a point of reference in measuring total length. On the other hand, the caudal appears to terminate 31 mm behind the hypural, but upon careful scrutiny it can be seen that one or more of the uppermost rays extend for 38 mm behind the hypural.

David's (1943) description of *E. manni* was based on a composite of several specimens representing at least two species and should be regarded as generally unreliable for characterizing the species.

ECLIPES EXTENSUS JORDAN, 1921

The type specimen of *E. extensus* (Jordan's No. 716) is the "tail only of a long and slender fish." The hypural elements are in such a poor state of preservation that we were unable to determine what direction was dorsal, an opinion shared by E. H. Ahlstrom (personal communication). It appears to be a gadoid, but there are no characters which will permit assignment to a particular gadoid family. The long slender vertebrae and strong neural and haemal spines differ strikingly from those found in the other three species ascribed to genus *Eclipes*.

ACTUARIOLUM BICAUDATUM (FROST, 1924)

In describing this otolith from New Zealand, Frost (1924) noted that it "resembles in a remarkable way the otolith of the living New Zealand species *Physiculus* [= *Pseudophycis*] *bacchus* [*sic*]." The broadly triangular, flared anterior end of this fossil resembles superficially the configuration of *Auchenoceros* sagittae, but the very short ostium precludes its being congeneric. Karrer (1971) proposed the name *Actuariolum* for this fossil and placed it in her *Pseudophycis*-group, but we believe the very short ostium of the fossil sagitta negates affiliation with *Pseudophycis*. In fact *A. bicaudatum* has sufficient anomalous characters to warrant establishing a separate group for it and *A. terakohensis* (Frost, 1933). The type series (three otoliths) is from a Pukeuri road cut, north Otago, in the Rifle Butts Formation, Awamoan Stage, Pareora Series and is Lower Miocene in age (J. A. Grant-Mackie, personal communication).

ACTUARIOLUM TERAKOHENSIS (FROST, 1933)

This otolith described (as *Physiculus terakohensis*) from "the unique holotype" is the basis for dating family Moridae from the Oligocene (Berg, 1940). Karrer (1971) recognized its erroneous placement with *Physiculus* and assigned it to her new genus *Actuariolum*. The holotype is from the Golden Bay Cement Company's marl pit at Tarakohe, Nelson, in the Tarakohe Mudstone, Altonian Stage, Southland Series which is Lower Miocene in age, not Upper Oligocene as originally reported by Frost (J. A. Grant-Mackie, personal communication).

While in New Zealand, one of us (Fitch) examined more than a dozen otoliths of *A. terakohensis* in the University of Auckland collections. All of these were from the Paratoetoe Formation (Lower Miocene) at Parengarenga Harbor on the North Island; otoliths associated with them included myctophids, berycids, bregmacerotids, macrourids, gonostomatids, congrids, and other deepwater forms as well as a few shallow-water species.

LOTELLA ANDRUSSOVI (BOGACHEV, 1933)

This species was assigned to genus *Brosmius* by Bogachev (1933) on the assumption that it had but a single, elongate undifferentiated dorsal fin. Danil'chenko (1953) determined that it did in fact have two dorsal fins, and because of the

two dorsal fins, a lack of teeth on the vomer and palatine bones, and other similarities with his fossil *L. smirnovi,* he placed it in genus *Lotella.* The type specimen (from middle Miocene) is in the form of a well-preserved double impression about 90 mm long, but lacking the anterior part of the head (Danil'chenko, 1960). Two other specimens, from the Tarkhan Beds of the Kerch Peninsula, were available to Danil'chenko (1960), but his description fails to mention the dentition. Positive assignment to family Moridae will necessitate finding a skeletal imprint with otoliths in situ or with a discernible morid caudal complex. Even then it cannot be assigned to *Lotella* unless the dentition that is characteristic of this genus can be observed.

ECLIPES SANTAMONICAE DAVID, 1943

The type specimen of *E. santamonicae* (David's No. 10223), now in the collection of the Natural History Museum of Los Angeles County, is a badly fragmented, poorly preserved gadoid, on which indelible brown ink has been used to draw in missing parts and to highlight others. Not only has the type slab been retouched, the photograph of the altered type (Figure 4, Plate 5: David, 1943) has been further retouched.

A careful comparison of the types of *E. santamonicae* and *E. manni* leads us to believe that they are conspecific; thus, *E. santamonicae* is relegated to the synonymy of *E. manni.* It is not a morid.

ONOBROSMIUS OLIGOCAENICUS BOGACHEV, 1938

Danil'chenko (1960) noted a marked similarity between some species of *Onobrosmius* and the fossil species referred to *Lotella,* and reported that among the few but conspicuous differences between *Onobrosmius* and *Lotella* are a slightly bipartite dorsal fin, wider pectorals, and particularly a greater number of pelvic fin rays in *Lotella.* Interestingly, he ascribed eight pelvic fin rays for both *L. smirnovi* and *L. andrussovi,* whereas he noted "V 7-8" for *Onobrosmius oligocaenicus.*

As with the description of *O. elongatus,* no character reported for *O. oligocaenicus* is diagnostic for family Moridae. *O. oligocaenicus* occurs in the Zuramakent Horizon, Upper Maikop, and according to Danil'chenko (1960) the fauna of this horizon cannot be compared with the fossil fauna of any other region, so the problem of its absolute geologic age remains obscure. Although the Zuramakent Horizon has been variously placed in Lower Miocene and Upper Oligocene, we believe from available evidence that it could be no older than Lower Miocene at most.

LOTELLA SMIRNOVI DANIL'CHENKO, 1953

In assigning this species to *Lotella,* Danil'chenko overlooked the very characteristic dentition of the genus: an outer row of widely spaced large teeth and an inner band of small teeth. According to Daniel M. Cohen (personal communication) the dentition of *L. smirnovi* is readily visible and is not as described above. Although there is nothing in the type description that would rule out assigning *L. smirnovi* to family Moridae, Daniel M. Cohen (personal communication) said that "the tail appears to have been regenerated, so I cannot be absolutely certain that it is a gadoid." In light of these anomalies it will be necessary to reevaluate *L. smirnovi* using irrefutable familial and generic characters, if such can be found on the available imprints.

L. smirnovi occurs in the same horizon as *Onobrosmius oligocaenicus,* and, as noted above, there is no substantial evidence that this horizon is older than Lower Miocene.

STRINSIA SOBIEVI DANIL'CHENKO, 1953

In his original description, Danil'chenko placed this fossil in family Moridae and stated that the holotype, a double impression 40 mm long, is similar to the Upper Miocene *S. alata* Steindachner which is known only from fragments of the head and forward part of the body. Subsequently, with additional material at hand, he designated *S. sobievi* as the type species for a new genus, *Protobrotula,* and moved it into family Brotulidae (Danil'chenko, 1960). Daniel M. Cohen examined Danil'chenko's material of this species and informed one of us (Fitch) that

"*Strinsia sobeivi* is based on very faint impressions [and]. . . I cannot say what it is." In view of the fact that the type of the genus *Strinsia* is a macrourid, that Steindachner's *S. alata* cannot be located, that Danil'chenko has moved his *S. sobievi* from family Moridae into family Brotulidae, and that diagnostic features cannot be found on the available material representing this species, it seems unlikely that this fish is a morid.

LEPIDION MIOCENICA SATO, 1962

Although this Miocene fossil from Japan probably is a gadoid and may be a morid, characters which could validate its assignment to family Moridae are either lacking or cannot be seen in the unique holotype. The vertebrae behind the second dorsal fin base are missing, otoliths are not mentioned and apparently were dissolved during fossilization, and if fontanelles ever were present in the exoccipitals they were rendered unrecognizable when this fish was crushed into a two-dimensional imprint.

In making his generic assignment, Sato (1962) states that "the present species is apparently referable to the genus *Lepidion* . . . in having [the] following important features: tail elongate and tapering posteriorly; two dorsals well developed together with the anal, and they are all composed of soft rays; anal fin is inserted far behind a perpendicular through origin of second dorsal fin base; snout is short and rather bluntly pointed in lateral view." Unfortunately, none of these characters is diagnostic of *Lepidion*, either by itself or in combination with the others. It would have been helpful to know if there were teeth on the vomer and the length of the anterior ray of the first dorsal fin (Norman, 1957).[5] Although Sato (1962) reported that the vomer was present, he failed to indicate whether it was toothed or naked. The anterior ray of the first dorsal fin is neither prolonged nor filamentous in the photograph of the type, but in his reconstruction Sato has made it filamentous.

[5] Norman, J. R. 1957. A draft synopsis of the orders, families and genera of recent fishes and fish-like vertebrates. British Museum (Natural History), London, 649 p. (Unpubl. manuscr.)

ODONTOBUTIS CF. *OBSCURA* HATAI, 1965

Apparently because of incorrectly identified comparative material Hatai (1965) assigned a "worn [morid] otolith measuring about 5 mm in length" from the Pliocene of Japan (Hamada sea cliff, Tanabu-machi, Shimo-Kita-gun, Aomori Prefecture) to family Eleotridae under the name *Odontobutis* cf. *obscura*. We do not know what species of morid he had for comparison [listed as *Odontobutis obscura obscura* (Temminck and Schlegel), and *O. o. yuriagensis* new subspecies], but the otoliths he illustrates appear to be identical to one reported by Fitch and Brownell (1968) from the stomach of a pygmy sperm whale harpooned off Japan. His fossil otolith has a bluntly rounded anterior end and differs in other features from those he affiliated it with, so it could not be identical. Based upon morid sagittae we have seen, Hatai's fossil otolith is most closely related to *Physiculus*, but correct generic placement must necessarily await comparison with morid species inhabiting the waters of Japan today. Karrer (1971) assigns this fossil to genus *Physiculus* (i.e., "ohne Zweifel der Gattung *Physiculus* angehören").

DISCUSSION

Based upon skeletal imprints, 12 fossil species have been assigned to family Moridae at various times in the past. Subsequently, one of these (*Merriamina ectenes*) was deemed conspecific with another (*Eclipes veternus*), and a second (*Strinsia sobievi*) was made the type of a new genus and moved into family Brotulidae. Our studies revealed that of the ten remaining species, one (*Eclipes santamonicae*) is conspecific with *E. manni* and three others (*E. veternus, E. manni*, and *E. extensus*) definitely are not morids. In addition we were informed that the type and only known specimen of *Strinsia alata* cannot be found, but since the tail portion of this imprint was never present and the remaining skeletal parts are not diagnostic, it could not be assigned to family Moridae even if the type were located. For the same reason (missing caudal complex), neither *Lotella smirnovi* nor *Lepidion*

miocenica can be retained in family Moridae with any certainty. Finally, the descriptions of the remaining three (*Onobrosmius elongatus, Lotella andrussovi,* and *Onobrosmius elongatus*) are all lacking in characteristics which are diagnostic of any gadoid family, and until or unless such features can be observed on the type specimens, the only reason for retaining them in family Moridae would be mere intuition.

Morids have also been reported in the fossil record from otoliths found in New Zealand, California, and Japan. One of these, reported as *Odontobutis* cf. *obscura* (an eleotrid) from the Pliocene of Japan, appears to represent an extant species of *Physiculus,* but no specific assignment can be made until comparative material from Japanese waters has been examined. All of the species known from otoliths are unquestionably morids.

On paleontological evidence, Danil'chenko (1960) reported that the Moridae constitute probably the oldest family of the order Gadiformes. He based this opinion on the belief that *Melanonus,* abundant in Oligocene rocks, was a morid, but Marshall (1965) removed *Melanonus* to its own family, and our investigations have revealed that none of the fossil morids, or presumed morids, is more ancient than Lower Miocene. Rosen and Patterson (1969) pointed out additional reasons for questioning morid antiquity and the logic of relating their ancestry to other gadoids.

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MARINE FISHERIES OF NEW YORK STATE[1]

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ABSTRACT

Review of the history of landings of fish and shellfish in the State of New York shows that the record since 1880 can be divided into three periods. The first was a period of development of coastal fisheries in shallow waters, which ended about 1930. The second, which lasted until the early 1950s, was a period of extension to fishing grounds farther offshore, the era of the trawl fisheries. The third was a period of steady decline in landings, still under way, characterized by a return to inshore resources.

The 90-year record has seen the rise and virtual collapse of the industrial fisheries of the State, steady decline of the oyster industry to a relatively minor status, and growth and decline of many other once-important fisheries. The variable level of total annual landings has been maintained by constant shifting from one resource to another as the stocks of each have declined in turn. This is a classic example of the evolution of a coastal fishery under a regime which offers no effective management.

Popular opinion is almost unanimous in blaming foreign fishing for the ills of the domestic fisheries. It is believed that unilateral extension of national jurisdiction would remedy the situation. In reality, although foreign fishing is not without effect, it impinges on relatively few of the coastal fishery resources of New York State. The major problems are domestic, and they will be most difficult to solve.

It seems particularly appropriate, in a volume which honors Dr. O. E. Sette, to discuss the marine fisheries of one of the northeastern States. It was in this general area that he did some of his earliest and best known scientific work, on *Scomber scombrus*, the Atlantic mackerel (Sette, 1930a, 1930b, 1931, 1932, 1933a, 1933b, 1934, 1938, 1943, 1950). It also is appropriate to use as basic data for this paper the published historical statistics on commercial fish catches, because for about 6 years Dr. Sette was Assistant in Charge of the Division of Fishery Industries in the United States Commission of Fisheries. In this capacity he was author of the annual reports of the Federal Government on commercial fishery landings (Sette, 1925, 1926a, 1926b, 1928; Sette and Fiedler, 1929).

When Dr. Sette first became responsible for gathering and publishing statistics on the commercial fisheries of the United States, only a few surveys of landings had been made and published. These began with data for 1880 and represented a few, usually widely scattered, years. The precision and completeness of these early records is questionable; but, when Dr. Sette began to gather the data for 1923, his well-known concern for accuracy and thoroughness began to be felt and his tenure in the 1920s marked the beginning of an almost unbroken series of annual reports on many aspects of the commercial fisheries of the United States, including landings by weight and value for each of the States.

Gathered, as they must be, by various indirect methods and by a relatively small force of field agents, these data cannot be completely accurate. It is obvious also that total landings are not very good indices of abundance of a species, for abundance can vary from many causes, such as changes in demand, or fishing effort, competition from other fisheries, and other economic forces. Yet no one would challenge seriously the value of these data as general indicators of trends in the fisheries and even as gross indicators of changing abundance. It is surprising that

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commercial landings have not been used more frequently to describe the condition of the fisheries of an area, for, used with caution and with an understanding of their limitations, these statistics can be most revealing (McHugh and Bailey, 1957). Considered in conjunction with existing knowledge of the biology and life histories of the stocks of fish and shellfish, they also can be valuable background materials for planning research, development, and management of the fisheries and the resources upon which they depend.

For these reasons, on beginning to examine the fisheries of a region it is useful to turn to the published record. It is not enough to consider total landings. The history of each fishery must be examined, for the species composition of the catch may be very different at different points on the time scale. For example, in the State of New York, as in many States, the ranking of species in landed weight in 1880 was greatly different than in 1970. American oyster (*Crassostrea virginica*), the dominant food species in 1880, was a very minor component of the catch in the 1960s. Surf clam (*Spisula solidissima*), not recorded in the catch until about 1900 and a minor resource until about 1950, now dominates.

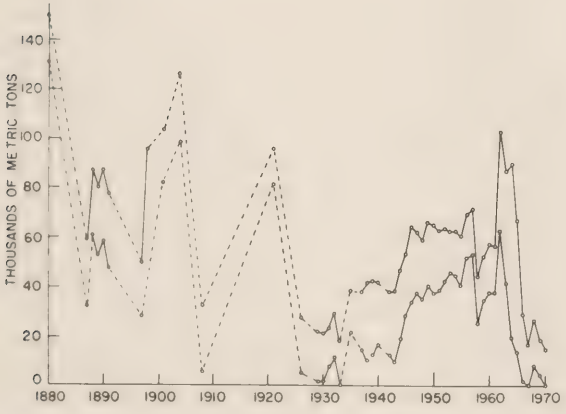

FIGURE 1.—Total annual commercial landings of fish and shellfish in the State of New York, 1880-1970. The lower line is the menhaden catch. In this, as in the other figures, broken lines have been used to join points between which one or more years' data are missing.

Examination of catches of a few years, selected at more or less regular intervals over the 90-year period, is not adequate to tell the whole story. Inevitably, some species, which were important for a while and then declined in their contribution to the total catch, will be missed. It is necessary to study the catch by species or by stock of fish for all years in which data are available. The work of Dr. Sette and his colleagues about 35 years ago, in improving the basis for collection of commercial catch statistics, has made this possible. The story that these records tell is most revealing in the light of present problems of the coastal fisheries and the steps that have been proposed to solve them.

I am indebted to Miss Karen Henrickson for her careful preparation of the illustrations.

HISTORY OF TOTAL LANDINGS IN NEW YORK

To analyze total landings intelligently the data must be separated into at least two subsets. In many coastal States, especially along the Atlantic and Gulf of Mexico coasts of the United States, industrial fishery resources dominate the marine commercial fish catch, and the history of total landings is largely a history of the industrial fisheries, primarily Atlantic menhaden, *Brevoortia tyrannus* (Figure 1). Total landings of food fish and shellfish have had a different history, which for New York apparently can be separated into three phases (Figure 2).

The first such phase, covering 1880 to 1926, was characterized by wide fluctuations in food fish landings in the State. Data are available for only nine scattered years, and their accuracy is not known, especially for the early years. The peak year in this period was 1908, with a reported food fish catch of about 54 million pounds (24,500 metric tons). More than 88% of this catch consisted of 13 genera: American oyster, weakfish (*Cynoscion regalis*), sea mussels (*Mytilus* and *Volsella* spp.), flounders (probably mostly summer flounder, *Paralichthys dentatus;* winter flounder, *Pseudopleuronectes americanus*; and yellowtail flounder, *Limanda ferruginea*), bluefish (*Pomatomus saltatrix*), Atlantic

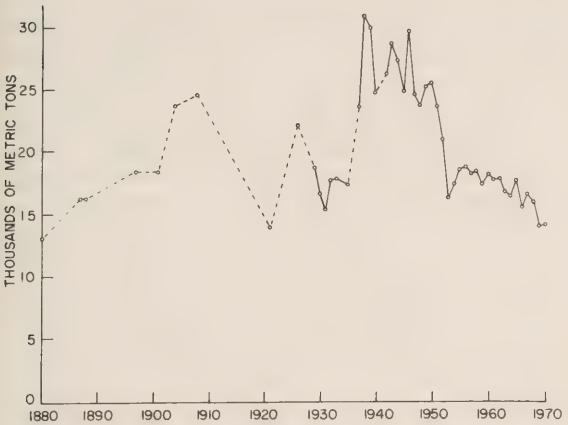

FIGURE 2.—Annual commercial landings of food fish and shellfish in the State of New York, 1880-1970.

cod (*Gadus morhua*), hard clam or quahog (*Mercenaria mercenaria*), scup (*Stenotomus chrysops*), butterfish (*Peprilus triacanthus*), and black sea bass (*Centropristis striata*). The low year, except for 1880, was 1921, with a reported catch of about 31 million pounds (14,000 metric tons) of food fish and shellfish. About 73% of these landings consisted of oyster, flounders, weakfish, scup, bay scallop (*Aequipecten irradians*), bluefish, northern lobster (*Homarus americanus*), hard clam, cod, and butterfish. The decrease was caused largely by sharp drops in landings of weakfish and mussels, and substantial drops in oyster, cod, and bluefish landings. By 1926 food fish landings had increased again to about 49 million pounds. The increase was mostly haddock (*Melanogrammus aeglefinus*), but landings of flounders and cod increased also. These increases were partially offset by a substantial drop in oyster production, but landings of weakfish, bluefish, and lobster dropped too.

The second phase was from 1929 to 1951. Landings were reported for almost every year of this period, which was marked by a sharp increase in food fish landings from 1935 to 1938, a 15-year period in which average annual food fish landings were about 58.4 million pounds (26,500 metric tons), and an equally sharp decline from 1950 to 1953. Most of the increase from 1935 to 1938 was caused by an increase in landings of haddock, cod, flounders, silver hake (*Merluccius bilinearis*), and butterfish, species caught primarily in trawls. Production of oyster meats also increased by nearly 4.5 million pounds (2,000 metric tons) from 1935 to 1938, as the highly mechanized oyster planting industry reached its full development. This almost doubled oyster production in the State and introduced a period of prosperity in the local oystering industry which lasted for more than 15 years.

The years of highest landings of food fishes in New York State, 1938 to 1946 inclusive, were unusual years for the fishing industry everywhere. Toward the end of this period, especially, demand for fish was high because meat rationing was in effect in the later years of the war. No price controls or rationing were imposed on fishery products. Thus, fish prices were high, and the incentive to go fishing was great. For 11 of the 13 years between 1938 and 1950 inclusive New York landings of food fish and shellfish were greater than ever before or since in recorded history, and it is probable that this could be said of 1941 also, a year in which no record of landings was made. The abrupt drop in landings which began after 1946 probably was stimulated by three factors, declining prices of fish as meat became more available after the war, increasing costs, and declining abundance of some of the major species.

Declining abundance of some species was becoming evident during the war. Although demand for fish was high, and prices good, the species composition of the catch was changing during this period of maximum landings and increased fishing effort. Catches of cod, flounders, haddock, butterfish, and sea scallop dropped substantially, and oyster production was down considerably also. The high levels of catch were maintained by increases in landings of hard clam and surf clam, northern puffer or swellfish (*Sphoeroides maculatus*), weakfish, and scup. Thus, the fisheries of the State were shifting from resources taken mainly on the high seas to species of the coastal zone.

The third phase, from 1952 to 1970, was a period of gradually declining landings. In the

first 10 years of this period the average annual landings of food fish and shellfish were about 40.4 million pounds (18,300 metric tons), and in the last 9 years about 35.7 million pounds (16,200 metric tons). Species which during the war began to contribute less to the catch continued in general to decline in importance; but the most spectacular declines were the virtual collapse of the two most important fisheries of the State, the oyster and menhaden industries.

INDUSTRIAL FISHERIES

Industrial fisheries have been relatively important along the northeastern Atlantic coast of the United States for a long time, although the peak of landings was not reached until about 1955. The principal species, and for most of the period of record the only industrial fishery resource of importance, has been the Atlantic menhaden. The period of greatest development of the Atlantic coast menhaden fishery came with the decline of the Pacific sardine (*Sardinops sagax*) fishery on the Pacific coast. Indeed, the recent history of menhaden landings shows a remarkable parallel to the rise and fall of the Pacific sardine fishery, with a time lag of about 20 years (McHugh, 1969b). There is no reasonable room for doubt that the principal cause of the decline in the Atlantic menhaden fishery was overfishing, as has been established for the Pacific sardine fishery (Murphy, 1966). It would have been prudent, for want of better information, to manage the menhaden fishery in the light of the extensive historical and scientific knowledge of the sardine resource, but for various reasons this was not done. The work of Dr. Sette and his associates on the sardine resource and its fishery (see, for example, Sette, 1969) could have provided valuable guidance for research and management of menhaden fishing if it had been heeded on the Atlantic coast. The Federal Government program on the Pacific sardine was started by Dr. Sette in 1948, and the results of this work, coupled with extensive studies begun much earlier by the State of California, have provided detailed documentation of the effect of fishing on the sardine resource. Although

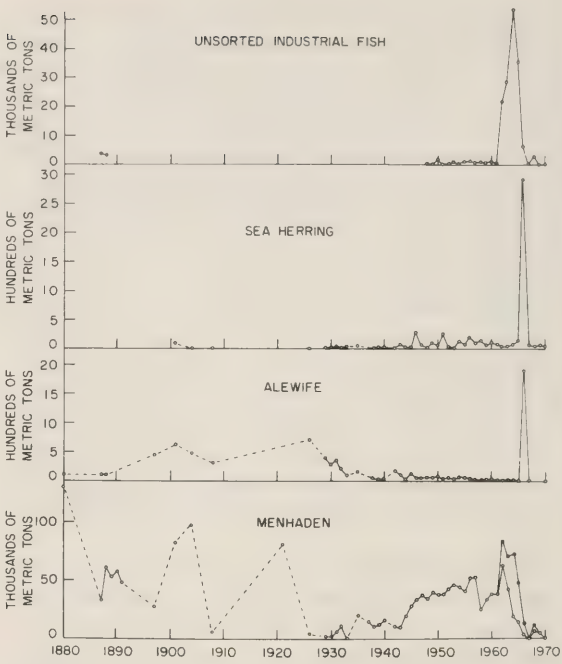

FIGURE 3.—Annual landings of industrial fishes in the State of New York, 1880-1970. The lines joining the black circles at the right of the menhaden graph represent total landings of all industrial species.

it is virtually certain that overfishing was the primary cause of the decline of both fisheries, the tendency of both resources to fluctuate widely in abundance from natural causes was an important contributing factor, which made overfishing inevitable.

The decline of the menhaden fishery north of Chesapeake Bay has been much sharper than to the southward. In New York the fishery is almost defunct (Figure 3). This decline could have been predicted with some assurance from the similarity of life histories of Atlantic menhaden and Pacific sardine and from the similar early collapse of the Pacific sardine fisheries in the north.

To state the background briefly, although both species spawn sometimes in waters near the northern parts of their ranges, the principal spawning areas are to the south, off southern California and Baja California, and to the south of Chesapeake Bay. Each year the fish make a

northward migration in spring and return in fall, and as they grow older they move farther north. Menhaden caught north of Chesapeake Bay usually are large, mature fish, most of which have had an opportunity to spawn at least once. It is probable that if menhaden fisheries had not developed south of Delaware Bay, the northern fisheries could have continued forever. It is certain that the abrupt decline in New York waters would have been slowed, if not prevented altogether. The resource would, of course, continue to fluctuate widely in abundance from natural causes, but the danger of overfishing probably would have been much less. The intense menhaden fishery in Chesapeake Bay, which now takes almost exclusively immature fish in their first and second years of life, reduces the life expectancy so greatly that few fish live long enough to migrate farther north. Thus, the collapse of the menhaden fishery in New York waters, like the early collapse of the sardine fishery in northern California and higher latitudes, was caused not so much by local overfishing, but by overfishing by other fleets in the waters of other States to the southward.

Menhaden landings in New York first began to decline in 1958. In 1959 a sharp increase in catches of menhaden in local pound nets heralded a brief increase in abundance, caused by unusually successful spawnings to the south. By 1962 menhaden landings in the State had risen to the highest level in recorded history since 1921. But the drop in 1958 had stimulated development of a new industrial fishery on mixed fish caught in otter trawls (Figure 3). This fishery for a while maintained the supply of industrial fish despite the rapid decline in menhaden landings after 1962, but the last year of substantial trawl catches of industrial fish was 1965. The decline of this trawl fishery had two principal causes, reduced abundance of fish on the grounds frequented by the fleet which was landing its catch in New York and return of most of the vessels to their home base in Rhode Island when the reduction plant at Point Judith opened (Smith, 1967).

In 1966, in a last desperate attempt to find alternate resources, the purse seine fleet made substantial catches of alewives (*Alosa pseudoharengus*) and Atlantic herring (*Clupea harengus*). The total catch of these two species (Figure 3) rose to more than 10 million pounds (4,600 metric tons), several times greater than any other year in recorded history. But this was a relatively small supply of fish for the menhaden plants, and the fishery lasted for only 1 year. The industrial fishing and processing industry of New York State has been virtually non-existent since 1966. The remaining plant on Long Island has closed, and the relatively few menhaden now caught in New York waters are taken to New Jersey for processing.

FOOD FISHERIES

As already mentioned, the history of the food fish and shellfish industry of New York State can be divided into three periods. Table 1 shows the relative and the absolute importance of the major species in four periods. It is clear even from this condensed summary that the species composition of the catch and the relative importance of many of the species have changed in complicated ways. It requires detailed consideration of each of the important species to understand how complex these changes have been and what implications are contained in this history.

Four sets of statistics were used in compiling these summaries. The illustrations are based on the Statistical Digests published annually by the Federal Government. The latest available, when background material for this paper was gathered, was Lyles (1969), which contained data for 1967. Since the 1950's the State of New York and the Federal Government have jointly published New York landings. The latest available was Smith (1971), containing data for 1970. Data on total commercial catches in the general area, including foreign catches, were taken from annual statistical bulletins compiled by the International Commission for the Northwest Atlantic Fisheries (ICNAF). The latest available was for 1968 (International Commission for the Northwest Atlantic Fisheries, 1970). The latest compilation of marine sport fish catches available was for 1965 (Deuel and Clark, 1968). Some data now are available on the 1970 marine sport fishing survey, but these could not be obtained in time for inclusion here.

TABLE 1.—Average annual landings in metric tons of major species of fish and shellfish in the State of New York for four major periods in the history of the commercial fishery of the State. Ranks by weight in parentheses.

Species	1887-1926	1929-1935	1938-1951	1952-1970
Oyster	6,085(1)	3,180(1)	3,270(2)	500(8)
Bluefish	2,360(2)	410(11)	* (25)	270(13)
Weakfish	1,315(3)	454(10)	590(13)	* (26)
Flounders	1,180(4)	2,950(2)	4,405(1)	2,860(2)
Cod	1,090(5)	1,180(4)	1,405(6)	454(9)
Shad	865(6)	135(21)	680(12)	180(17)
Hard clam	770(7)	545(9)	2,495(4)	2,250(3)
Alewife	410(8)	225(15)	* (30)	135(19)
Butterfish	365(9)	680(7)	1,225(7)	770(7)
American eel	365(10)	180(18)	90(24)	90(21)
Haddock		2,045(3)	2,770(3)	* (27)
Sea scallop		910(5)	1,045(10)	1,045(5)
Tilefish		865(6)	180(18)	* (24)
Scup		590(8)	2,360(5)	4,040(1)
Squid		365(12)	365(16)	410(10)
Atlantic mackerel		270(13)	680(11)	90(20)
Silver hake		270(14)	1,180(8)	1,135(4)
Soft clam		225(16)	135(22)	* (22)
Northern lobster		225(17)	90(23)	270(12)
Sea bass		180(19)	450(14)	270(14)
Surf clam		135(20)	1,135(9)	910(6)
Pollock		135(22)	* (28)	* (32)
Blue crab		90(23)	* (34)	* (30)
Atlantic bonito		90(24)	* (29)	* (29)
Sea mussels		* (28)	180(20)	* (25)
Red hake		* (29)	180(17)	180(16)
Striped bass		* (33)	180(19)	365(11)
Atlantic herring		* (37)	90(24)	225(15)
Northern puffer		* (58)	410(15)	180(18)
Flounders:				
Yellowtail			1,890	1,090
Winter			1,315	725
Summer			1,180	1,090

* Denotes average annual landings of less than 50 metric tons.

Domestic commercial fishery statistics are listed by States, but those of ICNAF and recreational fisheries are not. ICNAF added a new statistical area in 1966, which includes approximately the coastal and continental shelf waters from Rhode Island to Cape Hatteras, commonly referred to as the Middle Atlantic Bight. Prior to that time ICNAF statistics included only catches from Georges Bank north. Deuel and Clark (1968) reported sport fish landings by broad areas of coastal waters. Sport catches from waters off New York were included in the New England region.

For these reasons it was not possible to make direct comparisons of domestic commercial, foreign, and recreational catches for any single year. This is why the text follows the rather artificial device of comparing domestic commercial catches for 1970 with foreign catches for 1968 and recreational catches for 1965. This also is why, in comparing commercial and recreational landings, it was necessary to use the catch for the entire Atlantic coast north of Cape Hatteras.

OYSTER

Infrequent records of oyster production prior to 1929 show that landings probably were at a maximum in New York late in the 19th century and in the first decade of the 20th (Figure 4). Annual landings from 1887 to 1908 inclusive ranged from about 13 to 20 million pounds of meats (6,000 to 9,000 metric tons) and averaged over 15 million (7,000 metric tons). Thereafter, oyster production declined rather steadily

FIGURE 4.—Annual landings of oyster in the State of New York, 1880-1970.

except between 1926 and 1952 inclusive, when the trend was not obvious. Annual production in this period fluctuated between about 5 and 10 million pounds of meats (2,300 and 4,500 metric tons), and the average was somewhat more than 7 million pounds (3,200 metric tons). Although average landings in this intermediate period were only about half those reported at the turn of the century, this was in many ways the heyday of oystering in New York, despite closing of some once important grounds by pollution. Especially in Long Island Sound, this was the most highly mechanized and advanced form of oyster farming on the Atlantic and Gulf of Mexico coasts. After 1952 oyster landings in New York dropped sharply, and since 1959 annual production has been less than a million pounds of meats (less

than 450 metric tons). The low point was reached in 1967 with total production of only about 100,000 pounds of meats (45 metric tons).

The principal cause of the collapse of the New York oyster industry was a massive invasion of sea star (*Asterias forbesi*) in the 1950s. Favorable environmental conditions for this predator led to an extremely high survival of young sea stars, and the industry was unable to cope with this added predation, even with the relatively successful control measures that it had developed previously. Recovery has been slow because many other natural and man-made problems exist, including oyster drills (*Urosalpinx cinerea*, and to a lesser extent *Eupleura caudata*), unpredictable effects of storms, and a highly variable and reduced supply of young oysters. Wallace (1971) has cited water pollution as one of the major problems of the oyster industry in New York, but he voiced great hopes for hatcheries, four of which now are producing seed in New York. By 1970 oyster production in the State had increased fivefold, but still only to about half a million pounds of meats (230 metric tons). Time will tell whether hatcheries are the answer to the problems of the industry. The idea certainly is not new. The first oyster hatchery in New York was in operation in 1921 (New York Conservation Department, 1969). MacKenzie (1970) has suggested that natural setting is adequate to supply the needs of the industry for seed, if adequate measures are taken to eliminate mortality from siltation, predators, and careless handling. The feasibility of these methods of rehabilitating the oyster industry, no matter how valid they may be biologically, needs to be tested by economic studies.

SOFT CLAM

Traditionally a popular seafood in New England and the middle Atlantic region, the soft clam (*Mya arenaria*) has produced steadily decreasing landings in New York (Figure 5). Production in 1880 was reported as more than 3 million pounds of meats (1,370 metric tons). Average annual landings for years on record from 1887 to 1908 inclusive were just under 1 million pounds

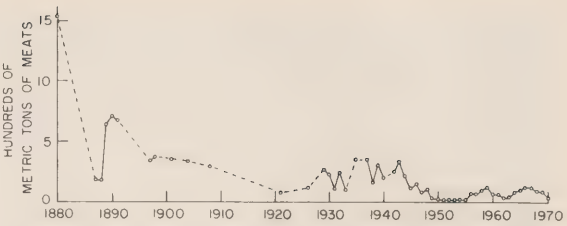

FIGURE 5.—Annual commercial landings of soft clam in the State of New York, 1880-1970.

(450 metric tons), from 1921 to 1945 inclusive less than half a million (200 metric tons), and from 1946 to 1970 less than 200,000 pounds (90 metric tons). To some extent the decline may have been caused by the long-term rise in water temperatures which in New England led to increased predation by green crabs. Wallace (1971) has attributed the decline in production to "pollution and physical changes in the estuaries." The soft clam is a vulnerable, shallow water species, and there is little doubt that overharvesting and lack of adequate regulation of the fishery were important factors.

BLUE CRAB

In the waters of New York State the blue crab, *Callinectes sapidus*, is near the northern limit of its range. It has never been a major species in the catch in this area. Because the blue crab is highly variable in abundance from natural causes even in the center of its range (McHugh, 1969a), it might be expected to be extremely variable in New York waters, and the history of the commercial fishery suggests that this has been true (Figure 6). Landings have declined steadily, but irregularly, since the maximum recorded catch of about 1.6 million pounds (725 metric tons) in 1880. Catches rose briefly in the 1930s, to a recorded peak of more than half a million pounds (270 metric tons) in 1935, but after a minor upsurdge in the early 1950s the fishery collapsed. No commercial catch has been recorded since 1961.

In Chesapeake Bay, with major fluctuations, the blue crab catch has been increasing for about 35 years. It has been suggested that the increased catch has been caused by increased

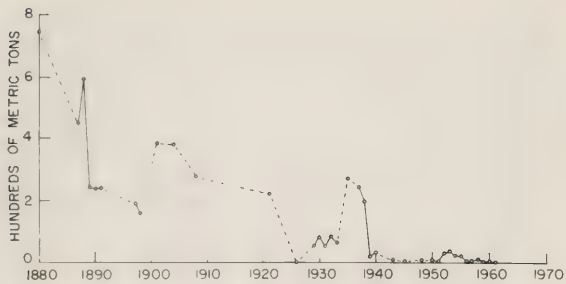

FIGURE 6.—Annual commercial landings of blue crab in the State of New York, 1880-1970.

abundance generated by nutrient enrichment in the estuaries (McHugh, 1969a), as was suggested also for striped bass (Mansueti, 1961). There is no direct evidence to support this hypothesis, but it is not untenable. Other than the decade of increased landings of blue crab which began about 1929 in New York, and a longer period of highly variable but substantially increased catches in the middle Atlantic region which ended in the late 1950s (McHugh, 1971),[3] there has been no similar continuing upward trend in blue crab production north of Chesapeake Bay. It is interesting to speculate that the enrichment of coastal waters and estuaries in the middle Atlantic region of the United States from domestic and industrial wastes may have stimulated blue crab production for a while, then became a limiting factor as eutrophication proceeded too far.

SHAD

The anadromous American shad (*Alosa sapidissima*), like the salmon, was a popular fish with the early settlers, wherever it was found along the Atlantic coast. Large catches have been reported in the early days from all major river systems. The Hudson River was one of the major producers, and maximum landings on record in New York State were more than 4 million pounds (2,000 metric tons) in 1889 (Figure 7). From 1880 to 1901 inclusive the average annual catch was over 3 million pounds (1,400 metric tons); from 1904 to 1935 inclusive it was only about one-tenth of this; then the catch began a steady rise to a peak of almost 3 million pounds (1,300 metric tons) in 1945, followed by an abrupt decline to less than a million pounds (275 metric tons) in 1949. Shad landings in New York for the last 3 years have been very much less than 100,000 pounds (about 16.5 metric tons).

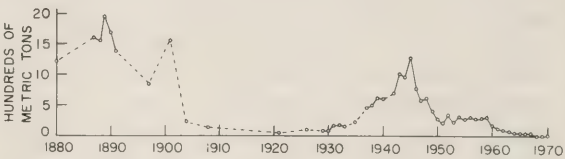

FIGURE 7.—Annual commercial landings of shad in the State of New York, 1880-1970.

This continued decline to what amounts to virtual collapse of the fishery is disturbing, especially in the light of the following statement by the Biological Section of the Scientific Committee of the Atlantic States Marine Fisheries Commission (1958a): "The Hudson River investigation has been completed and the fishery can now be managed successfully." What has gone wrong in little more than a decade?

The report cited above, and another special publication of the Atlantic States Marine Fisheries Commission (1958b) completely ignored the sharp increase in shad landings in New York, and indeed in the entire middle Atlantic region including Chesapeake Bay. At the time these reports were prepared the shad fishery of this entire region had swung from a maximum catch of nearly 36 million pounds (16,250 metric tons) in 1897 to a low of 5 million (2,270 metric tons) in 1935, to a secondary peak of about 12 million pounds (5,500 metric tons) in 1944 and again in 1945, and down again to less than 6 million pounds (2,700 metric tons) in 1958. It is difficult to reconcile the pompous statement quoted above with the past and subsequent history of the fishery (Figure 7). It is especially embarrassing to this author, who was chairman of the committee that issued these two reports.

[3] McHugh, J. L. 1971. Domestic wrangles and international tangles—the fisheries of the Middle Atlantic Bight. Unpublished manuscript, 237 p., filed at Woodrow Wilson International Center for Scholars, Washington, D.C.

The phenomenon of the rise and fall of the shad fishery in the Hudson River from 1924 to 1953 has been analyzed in some detail by Burdick (1954). He concluded that overfishing from 1941 to 1951 was responsible for the decline, which first became noticeable in 1946. He found no evidence that water pollution had any different effect on the shad stocks of the river during the period of rising catches than during the period after 1945. The overfishing was caused, according to Burdick, by the increased demand for fishery products during the war which led to relaxation of the fishing regulations (substantial shortening of the weekly closed season).

BLUEFISH

The bluefish (*Pomatomus saltatrix*) is a mysterious oceanic visitor to the coastal waters of New York. Commercial landings at the turn of the century (Figure 8) were 10 million pounds or more (average of about 4,800 metric tons for the 3 years 1897, 1901, and 1904). Early in the 20th century commercial landings dropped

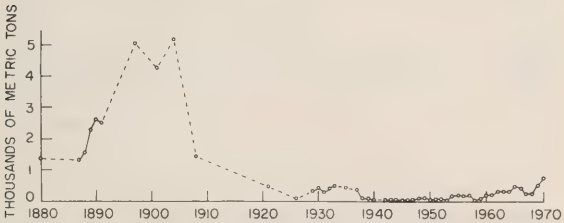

FIGURE 8.—Annual commercial landings of bluefish in the State of New York, 1880-1970.

abruptly, then rose from much less than a million pounds (135 metric tons) in the 1920s to about a million pounds (450 metric tons) in the 1930s, dropped to a very low level in 1940, and have been increasing, with some fluctuation, to nearly 2 million pounds (725 metric tons) in 1970.

Bluefish are an important and much sought after sport fish in the middle Atlantic region. Recreational catches for New York waters alone are not available in published analyses of data gathered by the Census Bureau (Deuel and Clark, 1968), but for the Atlantic coast as a whole the sport catch in 1965 was reported to be over 90 million pounds (41,000 metric tons), almost 15 times the total commercial catch of bluefish. Thus, it is probable that recreational fishermen take much more bluefish than commercial fishermen from New York waters. Briggs (1962, 1965, 1968) has confirmed that bluefish are among the most important species in the sport fisheries of Long Island.

Bluefish migrate to New York coastal waters in summer. Abundance is notably variable, but it is not understood clearly whether this is caused by real variations in abundance, or by a response to changing oceanographic conditions, or both. Abundance appears to have been increasing for the past 10 years or more.

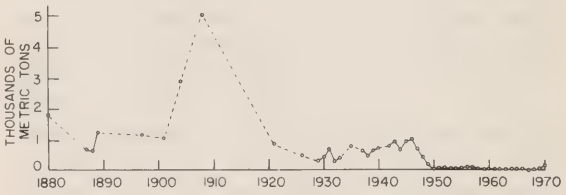

FIGURE 9.—Annual commercial landings of weakfish in the State of New York, 1880-1970.

WEAKFISH

The weakfish or gray seatrout (*Cynoscion regalis*) has been an important commercial species along the Atlantic coast. At the turn of the century most of the catch came from New York and New Jersey waters. Later the center of the fishery shifted southward to the area from Delaware Bay to the North Carolina sounds. The greatest landings recorded in New York were in 1908 (Figure 9) at over 11 million pounds (5,100 metric tons). Landings dropped to less than 1 million pounds (400 metric tons) in 1929, rose slowly to over 2 million (1,000 metric tons) in 1946, then dropped to very low levels after about 1948. The abundance of the species has declined along the entire Atlantic coast if commercial catches are a valid criterion. Recently, however, it apparently has been more abundant in the coastal waters of New York, especially in sport

fish catches. According to Perlmutter, Miller, and Poole (1956) weakfish available to New York fishermen belong to two distinct stocks, those which spawn locally and those which are southern spawned. These authors said that weakfish are abundant off New York only when the southern stock is large.

The recreational catch of weakfish in 1965 was estimated to be only 178,000 pounds (81 metric tons). It probably was considerably greater than this in 1970, but it appears that this is primarily a commercial species still.

The reason for the great decline in catches of weakfish is not known. Off Virginia in 1936 it was about 10 times as abundant as it was in 1946, according to the catch rate in pound nets (McHugh and Bailey, 1957). The increased catches in New York in the 1940s probably were caused by the increased demand for fish during the war, as already mentioned for several other species. Weakfish have been taken by trawlers in relatively deep water in winter, but the species has not been recorded in foreign catches off the Atlantic coast. Large numbers of young fish are killed by shrimp trawls in the Carolinas and in pound nets in Chesapeake Bay. Some people believe that this attrition has been responsible for the decline, but this source of mortality must have declined with the decline of the Atlantic coast pound net and shrimp fisheries.

SEA MUSSEL

Mussels are not in great demand as human food in the United States. Landings in New York State have been relatively small, seldom exceeding 1 million pounds of meats (500 metric tons). In 1908, however, a catch of over 8 million pounds of meats (3,800 metric tons) was reported, and in the 1940s (Figure 10) landings increased for a few years, probably because mussels were valued as a source of Vitamin D during the second world war. This may be a valuable latent resource if markets can be developed. The possibilities for aquaculture also should be investigated. Very high yields have been reported with hanging culture of mussels in Europe.

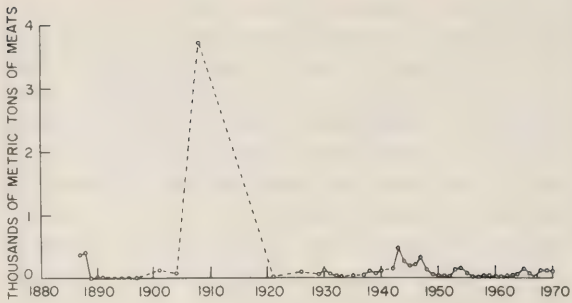

FIGURE 10.—Annual commercial landings of sea mussels in the State of New York, 1887-1970.

BAY SCALLOP

Bay scallop are in great demand and bring a high price. Landings in New York sometimes exceeded 1 million pounds of meats (520 metric tons in 1921) prior to 1932 (Figure 11), but the catch dropped sharply thereafter. The decline has been attributed to destruction of eelgrass

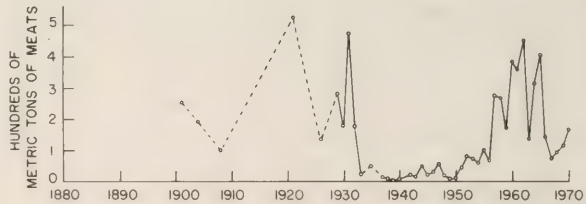

FIGURE 11.—Annual commercial landings of bay scallop in the State of New York, 1901-1970.

(*Zostera*) beds, by disease (*Labyrinthula*). As the eelgrass recovered, bay scallop became more abundant; and by 1962, landings in New York were up almost to a million pounds again. The abrupt decline to a low in 1967 may have been caused by overfishing.

HADDOCK

Haddock landings in New York apparently were at their greatest from 1908 to 1929 (Figure 12). The largest landing on record was in 1926 at about 17 million pounds (7,700 metric

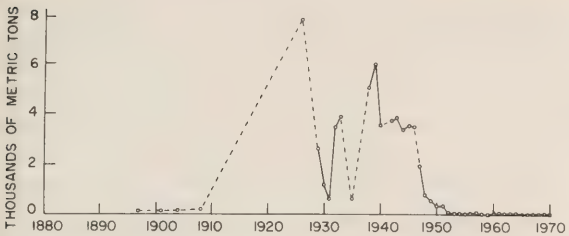

FIGURE 12.—Annual commercial landings of haddock in the State of New York, 1897-1970.

tons). Following a substantial drop in the 1930s the catch reached a secondary maximum in 1939, dropped to an average annual catch of about 8 million pounds (3,600 metric tons), to 1946 inclusive, then declined sharply, and remained extremely low for the last two decades. This decline of local haddock landings probably came about through the general decline of the New York trawl fleet after the war, for landings in New England, mostly from Georges Bank, remained remarkably steady from the late 1930s to the middle 1960s (Graham, 1968). Recent overfishing has brought the Georges Bank haddock stock to a very low level (Edwards, 1968), and it is unlikely that haddock will again become an important component of New York landings for some time, if ever.

TILEFISH

No record of tilefish (*Lopholatilus chamaeleonticeps*) landings in New York is available prior to 1929 in statistics published by the Federal Government. Yet Bigelow and Schroeder (1953) stated that 11,641,500 pounds (5,285 metric tons) of this species were caught off New England from July 1, 1916, to July 1, 1917. These authors concluded that the drop to less than half a million pounds (220 metric tons) in 1947 (about 42% of it in New York) was caused by a lack of demand.

The tilefish is of special interest to ecologists, although now a minor commercial species, because it inhabits a narrow band of ocean bottom at the edge of the continental shelf from Nova Scotia to southern Florida and in the Gulf of Mexico. Off New England and the middle Atlantic coast it is restricted to a zone of relatively warm water of about 8° to 12°C at depths of 82 to 360 m. Within 3 years after its existence was discovered in 1879 almost due east of New York Bight, the tilefish resource suffered a mass mortality. Large numbers of dead tilefish were reported floating at the surface over the edge of the continental shelf from off Delaware Bay to New England. The kill was attributed by Bigelow and Schroeder (1953) to a sudden shift or dissolution of this warm intrusion. The reduction in abundance was so drastic that no tilefish was taken in the area until 1892, and substantial commercial fishing on the resource did not resume until 1898. It is thus established that the tilefish is subject to very wide fluctuations in abundance from natural causes.

When tilefish first appeared in the commercial fishery statistics for New York State in 1929, landings were about 2.5 million pounds (1,180 metric tons). The catch fluctuated between 1 million (454 metric tons) and 2.5 million pounds in the period 1929 to 1935, then dropped sharply to nearly zero in the middle 1940s (Figure 13).

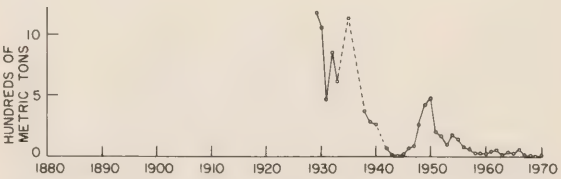

FIGURE 13.—Annual commercial landings of tilefish in the State of New York, 1929-1970.

A secondary maximum of just over a million pounds was reached in 1950, and subsequently landings in New York dropped steadily to a very low level. The collapse of this fishery in New York may have been caused by lack of demand, by the general decline of the trawl fisheries of the State after the war, by a natural decline in abundance, or by overfishing. Tilefish are not listed separately in the statistical bulletins of ICNAF, but are included under "other groundfish." In 1968 this category included a catch of 172,000 metric tons of mixed fish, which

could have included significant quantities of tilefish. A deep-sea sport fishery has developed recently (Richard H. Schaefer, personal communication).

COD

Cod, like many of the species caught principally or exclusively in otter trawls, was landed in maximum quantities in New York 30 to 35 years ago (Figure 14). The peak catch was about 8.5 million pounds (3,870 metric tons) in 1938, and landings declined sharply thereafter, as the trawl fishery of the State declined. The trend of New York landings of cod prior to 1940 was different from the trend of total U.S. catches of the species, which have declined irregularly since the last decade of the 19th century from 60,000 metric tons to less than 12,000 metric tons in 1953 (Graham, 1970). After 1940, cod landings in New York dropped at a fairly steady rate, from about 3 million pounds (1,450 metric tons) to less than half a million (200 metric tons) in 1970.

FIGURE 14.—Annual commercial landings of cod in the State of New York, 1880-1970.

The cod resource of the North Atlantic Ocean is tremendous, as demonstrated by the dominance of this species in landings from the ICNAF regulatory area. In 1968, for example, the catch of cod in this area was 1.86 million metric tons, about 48% of the total catch of all species from the area, which included at least 120 species of fish, shellfish, and other marine organisms of commercial value. Neither Graham (1968) nor Edwards (1968) considered that the cod stocks in the areas fished by Americans were overexploited. Edwards (1968) estimated that the standing crop in those areas was about 489 million pounds (222,000 metric tons), of which about 32% was being caught annually. Nevertheless, according to ICNAF annual reports pressure on the cod stocks is heavy, and there is some evidence that yields could be increased by increasing the mesh size of the trawls.

Cod is not the principal species sought by the U.S. fishing fleet but is taken incidental to the haddock fishery. A substantial sport fishery for cod has developed along the north and middle Atlantic coasts of the United States. The recreational catch in 1965 was estimated to be nearly 30 million pounds (13,580 metric tons).

FIGURE 15.—Annual commercial landings of butterfish in the State of New York, 1889-1970.

BUTTERFISH

The trend in landings of butterfish in New York (Figure 15) is not unlike the pattern for cod (Figure 14) and other trawl-caught species. The maximum catch was more than 5 million pounds (2,380 metric tons) in 1939. Thereafter, the catch declined irregularly to a low of about half a million pounds (240 metric tons) in 1970. The pronounced variations in catch were probably caused mainly by variations in success of spawning. The downward trend reflects the decline of the trawl fishery. Small panfishes like butterfish, which cannot be filleted and made into fish sticks or portions at reasonable cost, have declined in popularity as the frozen fish industry has developed. Reduced demand for such kinds of fish almost certainly has contributed to the decline of the New York trawl fisheries.

Relatively large quantities of butterfish are taken by foreign fishing fleets in international waters. In 1968 the total reported catch in the ICNAF statistical area was about 4,000 metric tons, somewhat less than half of which was caught by American fishermen. New York's share was only about 10% of the domestic catch.

Edwards (1968) estimated that the standing crop of butterfish off New England and New York was about 309 million pounds (140,300 metric tons) of which only about 3% is taken each year by the commercial fisheries. He considered that the resource is underutilized, mainly because it is a midwater species for which no effective fishing gear has yet been developed.

Schaefer (1967), sampling with a beach seine in the surf along the south shore of Long Island, found that butterfish were the most abundant species in his catches in 1961. In 1962 and 1963 they dropped to third and sixth place respectively, which may mean that this species varies widely in abundance from natural causes.

There is no recorded sport catch of butterfish, although it is known that they will bite on small baited hooks.

SILVER HAKE

Silver hake, often called whiting, is the most abundant groundfish on New England banks according to Edwards (1968). Demand for silver hake as a food fish is limited in the United States. Much of the domestic catch is used for animal food, and some as industrial fish. Edwards (1968) estimated that the standing crop on American fishing grounds in the middle 1960s was about 2.1 billion pounds (nearly a million metric tons) and that the average annual catch by all commercial fishing fleets was about 31% of the standing crop. Peak landings in New York were about 6 million pounds (2,690 metric tons) in 1943 (Figure 16). The catch declined to an average of less than a million pounds (420 metric tons) from 1948 to 1952, then rose and maintained an average annual level of about 2.8 million pounds (1,270 metric tons) for 16 years, from 1954 to 1969 inclusive. In 1962 foreign catches began to rise rapidly from previously

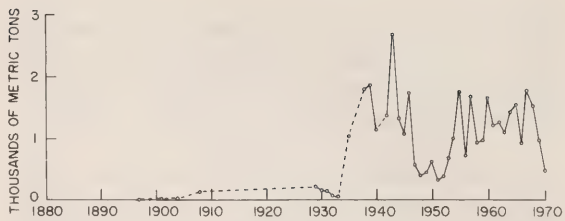

FIGURE 16.—Annual commercial landings of silver hake in the State of New York, 1897-1970.

low levels. The total catch in the ICNAF area reached 373,000 metric tons in 1965, then dropped just as abruptly, but New York landings were not affected very much, nor were U.S. landings as a whole. Strong year classes apparently were produced in 1967 and 1968, which augurs well for the fishery in 1970 to 1972 (International Commission for the Northwest Atlantic Fisheries, 1969). The recent decline in New York landings can be attributed only to the decline of the local trawl fleet.

The sport catch of silver hake in the New England and middle Atlantic areas in 1965 was estimated to be about 6 million pounds (2,720 metric tons).

NORTHERN PUFFER

The northern puffer, or swellfish, although it is abundant from Cape Cod southward, was not considered to be an important food fish until meat rationing during the second world war stimulated the coastal fisheries. The greatest catch in New York waters was in 1945, when almost 2.5 million pounds (1,060 metric tons) were landed. Subsequently the catch declined to less than 200,000 pounds or about 70 metric tons (Figure 17), rose to a secondary maximum in 1963 (nearly a million pounds or 430 metric

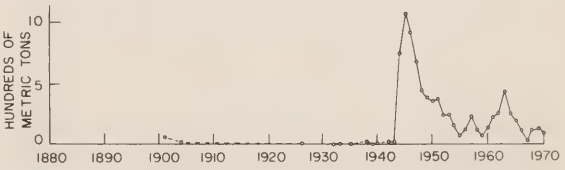

FIGURE 17.—Annual commercial landings of northern puffer in the State of New York, 1901-1970.

tons), and dropped off again. Until recently most of the catch has come from Gardiners and Peconic Bays; but as landings dropped in the middle 1960s, fishing effort shifted to the ocean off the south shore of Long Island and to a lesser extent into Long Island Sound.

Richard Miller, Executive Secretary of the Long Island Fishermen's Association (personal communication), says that the decline in New York landings of northern puffer was caused by the growing fishery in Chesapeake Bay (McHugh, 1969a), which led to a substantial decline in prices.

The declining catch of northern puffer in the bays of the eastern end of Long Island may have been caused by the decline of the pound net fishery, by overfishing, or by natural causes. The drop has been substantial, from a maximum of over 850,000 pounds (385 metric tons) in 1963 (over 90% of total commercial landings of puffers in New York) to 90,000 pounds (41 metric tons) in 1969 (less than 35% of total New York puffer landings). Recent development of fisheries for this species in the ocean and in Long Island Sound suggest that it may be generally an underexploited resource in the waters of the State.

The northern puffer is one of the more important species in the coastal sport fisheries of New York, although this is more by accident than by design. According to Briggs (1965) they are regarded as a nuisance, especially by flounder fishermen, who complain that puffers "steal their bait." Indeed, when puffers are abundant in Great South Bay, spring catches of winter flounders go down, not necessarily because they are less abundant but because puffers take the bait more readily and this discourages flounder fishermen. In the bays of eastern Long Island the catch of puffers by sport fishermen apparently has not had a great effect on the commercial fishery, for Briggs (1968) found that this was not a particularly important element of sport catches there.

The increase in commercial landings of puffers from 1960 to 1963 (Figure 17) probably was caused by a real increase in abundance. This is confirmed by two sport fishing studies. Briggs (1965) estimated that the sport catch of puffers in Great South Bay increased about fivefold from 1960 to 1962, from about 58,000 to about 314,000 fish. The sport catch was almost as high in 1963 as in 1962. Schaefer (1967) estimated the relative abundance of fishes in the surf zone on the south shore of Long Island and found that puffers were the most abundant species in catches of a beach seine in 1962 and 1963 (about two-thirds of all the fish caught), whereas in 1961 less than 1% of the catch had been puffers.

In 1965 it was estimated that about 26 million pounds (11,750 metric tons) of northern puffers were taken by sport fishermen along the middle Atlantic coast.

ATLANTIC MACKEREL

Once an important fishery, the domestic Atlantic mackerel industry has been producing for the last 15 years or more only about 3% of the maximum recorded catch in 1884 (Hoy and Clark, 1967). Landings of mackerel in New York have fluctuated more or less in proportion to domestic landings along the Atlantic coast as a whole. Most of the catch in New York now is made in pound nets, although gill nets at one time were the most important gear. Thus, to some extent the decline in New York landings (Figure 18) may have been caused by the decline of the pound net fishery. The demand for mackerel in the United States also is less than it was early in the century. Abundance varies widely from natural causes (Sette, 1938).

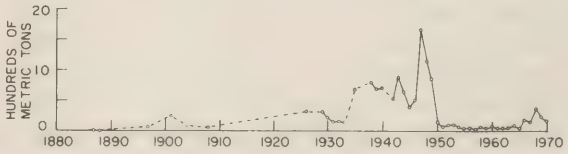

FIGURE 18.—Annual commercial landings of Atlantic mackerel in the State of New York, 1887-1970.

Mackerel are important in high-seas fisheries by foreign fleets. In 1968 the total catch reported from ICNAF statistical areas was 71,595 metric tons, of which only 3,001 metric tons were caught by American commercial fishermen. Thus, the present total catch by all nations is almost equal to the greatest domestic catch on

record. The estimated recreational catch in 1965 was nearly 19 million pounds (8,590 metric tons). It appears that the decline of the domestic mackerel fishery was a matter of declining demand and that sport fishermen and foreign fleets have willingly preempted the harvest.

Edwards (1968) noted that mackerel have not been abundant in the northwestern Atlantic recently, but that abundance has been increasing.

SEA BASS

Landings of sea bass in New York fluctuated around a level of about half a million pounds (225 metric tons) a year until 1943 (Figure 19), when the catch began to rise sharply, reaching a maximum of about 2.8 million pounds (1,270 metric tons) in 1951. Then the annual landings began to drop just as sharply, and they are still falling. Commercial landings in New York in 1970 were only about 70,000 pounds (32 metric tons). This is primarily a fish of shallow waters,

FIGURE 19.—Annual commercial landings of sea bass in the State of New York, 1887-1970.

and no landings have been reported by foreign fleets in the ICNAF statistical areas. Sea bass move offshore to deeper water in winter, and some may be included in the unidentified category. Most of the domestic commercial landings in New York are caught in otter trawls, and a substantial part of this sea bass catch comes from outside the 3-mile limit, if not beyond the zone of domestic fishery jurisdiction.

For the Atlantic coast as a whole the recreational catch of sea bass in 1965 was estimated to be nearly 11 million pounds (4,945 metric tons), more than 2.5 times the total commercial catch on the Atlantic coast in 1970. Partial surveys of the sport fisheries of Long Island, cited elsewhere, do not show that this is a very important recreational resource in this area.

The decline in sea bass landings in New York is attributable at least partly to the decline of the trawl and pound net fisheries. Landings in New Jersey and the Chesapeake Bay States have declined also, but neither as abruptly nor as soon. It is not known whether the resource has been overfished, and it appears that to some extent the decline in commercial landings may have been offset by increased recreational catches.

FIGURE 20.—Annual commercial landings of sea scallop in the State of New York, 1887-1970.

SEA SCALLOP

The history of sea scallop landings in New York has been generally similar to the history of landings of the same species in New England (Graham, 1968). The recent sharp decline in New York landings (Figure 20) has the same causes as the similar decline of the U.S. sea scallop catch as a whole: increased catches by foreign fishermen, and generally poor survival after the last highly successful spawning which reinforced the scallop population on Georges Bank early in the 1960s. Sea scallop landings at Fulton Fish Market declined abruptly after 1965, and by 1970 the number of trips by scallop dredgers landing their catch there had dropped considerably.

SCUP

As illustrated by Figure 21, scup became increasingly important in New York landings in the 1940s and 1950s, reaching a maximum of

FIGURE 21.—Annual commercial landings of scup in the State of New York, 1889-1970.

over 14 million pounds (6,490 metric tons) in 1958. In fact, scup ranked first by weight of all food fishes and shellfish landed in New York from 1953 to 1961 inclusive. The subsequent decline was abrupt, the catch dropping to just over a million pounds (545 metric tons) in 1970. Almost all of the catch was made by otter trawls, most of it beyond the 3-mile limit, and about half of it landed at Fulton Market in New York City. The causes of declining commercial catches are not understood at all clearly. The total domestic catch in 1970 was only about 10.5 million pounds (4,770 metric tons), less than what was landed in New York alone in 1958. The foreign catch in 1968 was only about 5 million pounds (2,255 metric tons). The total recreational catch in 1965 was estimated to be about 37.6 million pounds (17,075 metric tons).

Briggs (1968) found that scup were the most important species by numbers caught in the sport fisheries in the bays of eastern Long Island. In 1965, for example, he estimated that the total catch in this small area was over a million fish, 44% of the catch by numbers. The following year the sport catch in the same area was reduced by nearly 50%. Finkelstein (1969) noted that from historical times scup were known to go through extreme variations in abundance, from great abundance to such scarcity that the species was virtually absent for years.

Edwards (1968) estimated that the standing crop of scup from New York Bight north was about 66 million pounds (30,000 metric tons) per year from 1963 to 1965. Average annual commercial landings in the same period were about 10 million pounds (4,540 metric tons), and thus the commercial fisheries were taking only about 15% of the standing crop each year. It would appear from all these estimates and other data that if the decline in scup landings has been caused by fishing, the sport fisheries have been the principal contributing agent. However, it appears equally likely that variations in spawning success could be the cause. Of course, when the resource is at an extremely low level of abundance, whatever the cause, it may be much more vulnerable to heavy fishing intensity.

FLOUNDERS

The major species of flounder in the New York catch are yellowtail, winter flounder or blackback, and summer flounder or fluke. Other names which appear in United States or ICNAF statistics are gray sole (*Glyptocephalus cynoglossus*), which ICNAF calls witch; lemon sole, which is simply a winter flounder that weighs more than 3½ lb. (1.6 kg); dab (*Hippoglossoides platessoides*) which is called American plaice by ICNAF; and hogchoker (*Trinectes maculatus*). The last two, and perhaps some other species, may be included under unidentified categories in New York landings. This vernacular and scientific terminology is so confusing that these names have been listed and properly paired off in Table 2 as compared with the official listing of the American Fisheries Society (Bailey, 1970).

Individual species of flounder were not identi-

TABLE 2.—Common and scientific names of flounders as used in domestic (NMFS) and international (ICNAF) statistics, and as endorsed by the American Fisheries Society (AFS).

Common name	Source	Scientific name
Yellowtail flounder	NMFS, ICNAF, AFS	*Limanda ferruginea*
Blackback flounder	NMFS (under 3½ lb.)	
Lemon sole	NMFS (over 3½ lb.)	*Pseudopleuronectes americanus*
Winter flounder	ICNAF, AFS	
Fluke	NMFS	
Summer flounder	ICNAF, AFS	*Paralichthys dentatus*
Gray sole	NMFS	
Witch	ICNAF	*Glyptocephalus cynoglossus*
Witch flounder	AFS	
Dab	NMFS	
American plaice	ICNAF, AFS	*Hippoglossoides platessoides*
Hogchoker	NMFS, ICNAF, AFS	*Trinectes maculatus*

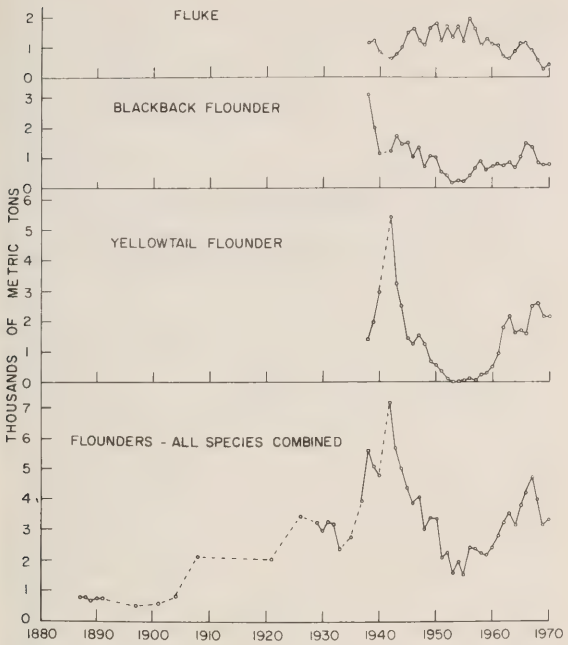

FIGURE 22.—Annual commercial landings of flounders in the State of New York, 1887-1970.

fied in U.S. statistics until about 1938 (Figure 22). Total landings of all flounder species in New York have two maxima, one at nearly 16 million pounds (7,130 metric tons) in 1942 and the other at more than 10 million (4,720 metric tons) in 1967. Between these peaks the catch dropped off to an average annual minimum level of about 4 million pounds (1,850 metric tons) from 1951 to 1955 inclusive.

Most of this dip, and much of the subsequent rise, was caused by a wide oscillation in landings of yellowtail flounder (Figure 22) from about 12 million pounds (5,400 metric tons) in 1942 to virtually nothing in 1952 to 1957, then back to nearly 6 million pounds (2,565 metric tons) in 1968. Graham (1968) attributed these fluctuations to changes in abundance of yellowtail flounder, without citing causes. Royce, Buller, and Premetz (1959) went into the question in detail. Edwards (1968) estimated that the standing crop of yellowtail flounder in areas fished by Americans was 185 million pounds (84,000 metric tons). Average total landings from these same areas from 1963 to 1965 were more than 50% of the standing crop annually, which is the highest fishing rate for any species in the area.

Smith (1963, 1968, 1969) also noted the increasing abundance of yellowtail flounder in the 1960s on grounds frequented by New York fishermen. Despite an abrupt drop in numbers of trawlers landing their catches at Fulton Fish Market in New York City from 1960 to 1966 (a drop of approximately 80%) the weight of yellowtail landed nearly doubled. From 1960 to 1965 and 1966 the catch of yellowtail per trip rose from about 71 lb. to about 700 lb., a crude but fairly convincing index of increasing abundance. Lux (1969) presented evidence that dominant year classes spawned in 1958, 1959, and 1960 produced greater abundance of yellowtail on fishing grounds off New England from 1960 to 1963, but that abundance declined from 1964 to 1966. Alarmed at the heavy rate of fishing on this resource, ICNAF established catch quotas in 1970 aggregating 29,000 metric tons, and in the following year reduced this quota to 26,000 tons.

The yellowtail flounder is a species of relatively deep water. No catches were reported by sport fishermen in 1965.

Winter flounder landings in New York also declined from the 1930s to the early 1950s, then rose again. The domestic commercial catch dropped from nearly 7 million pounds (3,050 metric tons) in 1938 to about a third of a million (160 metric tons) in 1953, then back to slightly over 3 million (1,475 metric tons) in 1966. According to Poole (1969) winter flounders have been abundant recently in New York waters. He attributed the relatively small commercial landings in the State to restrictions on trawling which have been in effect for 25 to 30 years. This is primarily a fish of shallow coastal waters. In 1968 in the western North Atlantic foreign fleets took only 1,200 metric tons, as compared with a total domestic commercial catch of about 10,700 metric tons.

The total U.S. sport catch of winter flounder in 1965 was nearly 29 million pounds (over 13,000 metric tons). The species is important in the saltwater sport fisheries of the State.

Briggs (1962, 1965, 1968) found that about 1.5 million fish were taken in Great South Bay each year and about another million per year in Moriches, Shinnecock, Gardiners, and Peconic Bays. In 1964 to 1966 he found that winter flounders made up from 17 to 40% of the sport catch by numbers in the bays of eastern Long Island.

Edwards (1968) estimated that the standing crop of winter flounder in the northwestern Atlantic was about 185 million pounds (84,000 metric tons), about the same as the estimate for yellowtail. The rate of exploitation by commercial fleets, however, was considerably less, about 17% per year.

Commercial landings of summer flounders in New York (Figure 22) have followed essentially the same trend as commercial catches for the New England and middle Atlantic States as a whole, reaching a maximum in the 1950s and dropping off fairly steadily thereafter. Poole (1966) suggested that the increase in catch from 1938 to the 1950s was a result of increased fishing effort, not increased abundance. Commercial landings in New York are only about 20% of total commercial landings, and there is no reported foreign catch. The total recreational catch in 1965 was estimated to be nearly 35 million pounds (15,800 metric tons), about 6 times the total commercial catch of 5.7 million pounds (2,590 metric tons).

The summer flounder, like the winter flounder, is one of the most important sport fishes in New York waters. Briggs (1962) found that from 1956 to 1960 sport fishermen took about 1.5 million fish per year from Great South Bay alone. The New York State Department of Environmental Conservation has estimated that 1.7 million anglers fish each year in marine waters of the State (A. C. Jensen, personal communication). Their removals of summer flounder and other species are a very important part of total fishing mortality.

SURF CLAM

The surf clam fishery of the Atlantic coast began its period of major growth in the middle 1940s. Landings in New York (Figure 23)

FIGURE 23.—Annual commercial landings of surf clam in the State of New York, 1904-1970.

were relatively small compared with New Jersey, which reached a level of over 43 million pounds (19,600 metric tons) of meats in the late 1960s. But the fishery began off Long Island and shifted south later, as abundance dropped on local beds. The resurgence of the New York surf clam industry after 1958 came about through discovery of new offshore beds and development of more efficient harvesting gear. The future of the surf clam fishery of the State is uncertain because, like all molluscan shellfish resources, this species is extremely vulnerable to overharvesting, and controls are difficult to impose. The history of our shellfisheries is a history of overexploitation, and there is no reason to believe that the surf clam industry will be any exception. This industry grew because the soft clam and oyster industries inshore were declining. The great demand for clams and the current high prices will be great incentives to harvest known resources heavily and to seek out new grounds.

HARD CLAM

In landed value hard clams have been the most important commercial fishery species in New York since 1953. Landings reached a maximum in 1947 of nearly 11 million pounds (4,700 metric tons) of meats, then dropped abruptly to 1954 (Figure 24). Since the middle 1950s landings have climbed steadily from a low of about 2.5 million pounds (1,100 metric tons) in 1954 to nearly 8 million (3,590 metric tons) in 1970. Most of this increase has come from Great South Bay, which in 1959 produced about 1.5 million pounds (680 metric tons) of meats and in 1969 yielded more than 6 million pounds (2,860 met-

ric tons). This almost doubled the percentage contribution of Great South Bay to the total hard clam production of the State.

In discussing this growth of the hard clam industry in New York, Wallace (1971) pointed out that hard clams are much more adjustable to changing environmental conditions than oysters are, even in the larval stages. In Raritan Bay, once the center of oyster production in the area of New York Bight, hard clams still spawn successfully, although much of the bay is badly polluted and oysters are long since gone. He attributed the great rise in hard clam production in New York to a series of excellent sets in several bays on the south shore of Long Island.

FIGURE 24.—Annual commercial landings of hard clam in the State of New York, 1880-1970.

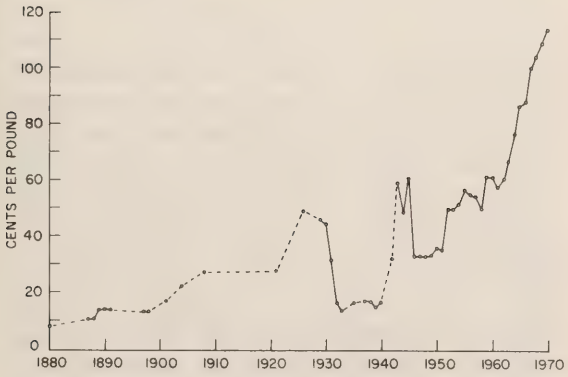

FIGURE 25.—Average annual landed value of hard clam meats in the State of New York, 1880-1970.

It would appear that part of the incentive to harvest clams more intensively has been provided by economic changes. As Figure 25 illustrates, the landed price per pound of hard clam meats has undergone some interesting changes over the years. Prices were high in the affluent days before the depression of the 1930s. In the 1930s they dropped to what probably would be a record low if the figures had been expressed in standard dollars. Prices rose sharply during the war and dropped as sharply immediately afterwards, as did the prices of most seafoods. Then in the 1950s the price of hard clams began to rise and the rise continued even more rapidly in the 1960s. This steady increase over a period of two decades can be explained only partially by the declining value of the dollar. The economic forces operating here must be largely if not completely the collapse of the oyster and soft clam industries and the growing affluence of most segments of the population, which seems always to stimulate demand for the more popular kinds of seafood, especially invertebrates.

STRIPED BASS

Commercial landings of striped bass (*Morone saxatilis*) in New York have been following an upward trend for the past 30 years or more (Figure 26). The same phenomenon has been observed along the Atlantic coast from Chesapeake Bay (McHugh, 1969a) north. The total Atlantic coast commercial catch in 1970 was about 10.5 million pounds (4,770 metric tons). The total

FIGURE 26.—Annual commercial landings of striped bass in the State of New York, 1887-1970.

estimated sport catch in 1965 for the Atlantic coast was between 5 and 6 times the weight of the commercial catch in 1970. The striped bass is an anadromous coastal species, and it has not been reported in catches of foreign fleets fishing offshore.

It seems unlikely that the great increase in striped bass landings over a 35-year period has come about through an equivalent increase in fishing effort, for this species has been popular as a commercial and recreational species for a long time. It has been suggested (Mansueti, 1961) that the species has been able to take advantage of increased nutrient loads in its nursery areas in Chesapeake Bay and elsewhere and that the increased catch has been largely, if not completely, caused by a real increase in abundance. This is entirely hypothesis, and data probably do not exist with which to test it. A small piece of suggestive evidence on a closely related species has been published recently. Tsai (1970), examining changes in fish stocks of the Little Patuxent River, Md., over a period of about a decade, found that some species had decreased considerably in abundance and others had increased. Among the species which had increased was the semi-anadromous white perch (*Morone americana*), which has a life history very similar to that of the striped bass during the first 2 years of its life when it does not move very far from the influence of the river in which it was born.

FIGURE 27.—Annual commercial landings of northern lobster in the State of New York, 1880-1970.

NORTHERN LOBSTER

Landings of lobster in New York also have been increasing for about 25 years. The maximum catch recorded in the earlier period was a little over a million pounds (470 metric tons) in 1921 (Figure 27). Then the catch fell off rather steadily to a low of about 150,000 pounds (64 metric tons) in 1945. In 1970 about 1.65 million pounds (750 metric tons) were landed in New York. The recent increase has been attributed to two phenomena. The first has been a general decline in coastal water temperatures for the last 10 years, which apparently has brought about a southward shift in the distribution of lobster and an increase in pot catches inshore. The second has been the increasing exploitation of hitherto unused lobster resources by trawls and pots in relatively deep water on the continental shelf. Graham (1968) stated that several inshore species along the Atlantic coast, including lobster, were producing catches at or beyond levels of maximum sustainable yield and that from now on the fluctuations in annual landings would be the result of fluctuations in recruitment or availability. The relation between the offshore and inshore lobster stocks is not completely understood, but recent investigations seem to be leading to the conclusion that the offshore lobster fishery may be harvesting a distinct stock. If so, it cannot yet be determined how large a catch it can sustain. The future of lobster landings in New York would appear at this time to be uncertain.

CONCLUSIONS

Consideration of trends in landings of some 28 species of marine fish and shellfish in the State of New York shows that the variable commercial fishery production of the State has been maintained by shifting from one species or stock to another as landings of each resource have risen to maxima and then declined, often to very low levels. The reasons for some of these declines or increases are known, but trends in landings of many species remain unexplained. At any point in time in the history of the coastal fisheries of New York, landings of some species are rising, and others declining, and there is no reason to believe that the pattern will change.

Even if a constituency receptive to rational management of the fisheries could be created, only a few of these resources are subject to control unilaterally by the State of New York. Most would require cooperative effort by all States through the waters of which the living resources migrate. Such cooperation has not been possible, although a mechanism exists in the Atlantic States Marine Fisheries Commission to provide cooperative management, if cooperation is really desired. To date, the Commission has demonstrated neither the desire nor the capability for joint management of coastal fishery resources.

In New York it can be expected that the situation may deteriorate further. Since 1962 the total weight of fish and shellfish landed in the State has dropped from more than 112,000 metric tons to about 14,500 metric tons, a decline of about 86% in 8 years. Most of this decline has been in the industrial fisheries, principally menhaden, but food fish landings have dropped also. Over the same period food fish and shellfish landings have dropped from about 18,000 metric tons to about 14,500 metric tons, a decline of about 21%. Indeed, the trend in seafood production has been downward for more than 30 years. Since 1938 New York seafood landings have dropped about 54% from 31,100 metric tons.

The species have been discussed approximately in chronological order of maximum commercial catch. This sequence was chosen because it illustrates rather nicely some of the reasons for the fluctuations observed. The sequence of rise and decline is typical of the evolution of coastal fisheries. Note that the first eight species of food fish and shellfish discussed, with two exceptions, are either molluscan shellfish or relatively nonmigratory species of shallow coastal waters, or anadromous. The two exceptions, bluefish and weakfish, although highly migratory, crowd into coastal bays and estuaries seasonally, where they are highly vulnerable to fishing. These are the kinds of fish and shellfish that support the early fisheries everywhere. They can be taken easily with primitive gear, sometimes without even the aid of a boat, and thus they are extremely vulnerable. To this group can be added menhaden and river herrings.

The next 12 species or groups of species, with only one exception, can be placed in two general categories: fish which come into coastal waters in abundance at times, but which also are abundant offshore; and those which seldom, if ever, come into coastal waters. Among these are demersal species like haddock and tilefish, densely schooling and highly migratory pelagic fishes like mackerel, or mollusks of relatively deep waters like sea scallop or surf clam. Many of these are taken by trawls, dredges, or purse seines, which require relatively large, powered vessels. This requires more capital investment and more manpower, hence calls for more organization and planning. These are the kinds of fish and shellfish to which coastal fishermen turn when the strictly coastal resources no longer can meet market demands. This is the typical evolutionary pattern of coastal fisheries, in which the fleets expand, increase in efficiency, and range out into the ocean and farther from their home bases. Almost all of these fisheries now are declining.

The one exception noted above is the northern puffer or swellfish, which as far as we know is very much a species of the coastal zone, living in shallow waters near shore. As such, it might be expected that the northern puffer fishery would have developed and declined much earlier than it did. The reason probably is that puffers have been regarded as repulsive, and their value as a first-class food fish was not recognized until recently. The well-known toxicity of tropical puffers also may have been a contributing factor.

The last three species discussed—northern lobster, striped bass, and hard clam—interestingly enough, are essentially resources of the coastal zone, which, like the puffer, would be expected to be subject to heavy fishing early, hence produce maximum landings early and then decline. Under most circumstances this might have been so, but special circumstances apply to each. With the lobster it is a matter of increasing availability in New York coastal waters in re-

sponse to natural environmental change and a new offshore lobster fishery on previously unexploited stocks. With striped bass it has been speculated that man-made changes in the environment actually have caused substantial increases in abundance. The recent increase in hard clam production may have a similar cause, but economic factors may also have played a part.

These trends and their relationships can be visualized more clearly by grouping species with more or less similar chronological patterns of landings (Figure 28). The seven groupings here illustrated were derived according to the decade in which the maximum catch was reached. The result forms almost a "textbook example" of the evolution and decline of a regional fishery.

Although the causes of most short-term changes in the landings are complex, the long-term deterioration of certain formerly important fisheries leads to the uncomfortable conclusion that lack of management and overfishing probably are important causes. The oyster, once by far the most important seafood resource in New York by weight or by landed value, today no longer ranks among the 10 most important species. Menhaden, an industrial fish, once the dominant species in New York landings by weight, and far outweighing all other species combined, today ranks eighth by weight, and the industry on which it was based is close to collapse. The oyster catch has been largely a cultivated crop, and in New York the efficiency of cultivation has been superior to that in any area except the Pacific Northwest. The recent decline of the industry has been caused by natural disasters with which the industry was unable to cope. But many of the problems could have been avoided by applying knowledge of the ecology of oysters, according to MacKenzie (1970), and the potential yield is far greater than the industry has ever realized. In other

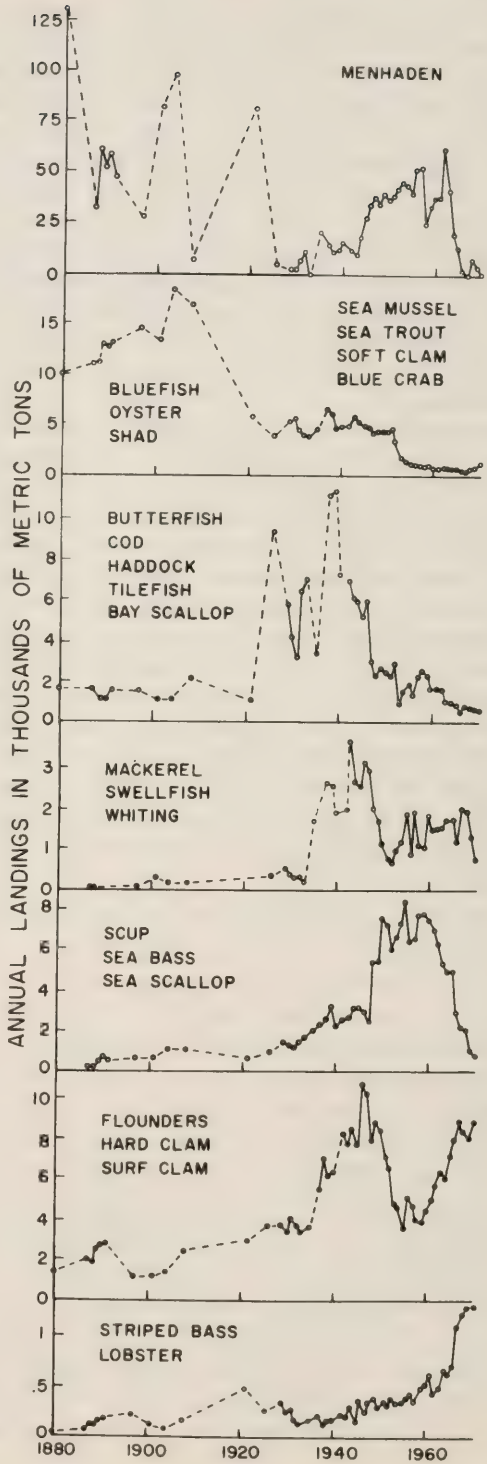

FIGURE 28.—Annual commercial landings of fish and shellfish in the State of New York, 1880-1970. The species have been grouped according to the decade in which the greatest landings were made and the groups are arranged approximately in chronological order of maximum landings. The two peaks in the second graph from the bottom do not represent a shift from one species to another. See text for details.

words, MacKenzie has said that although the methods used by oyster planters in New York were relatively efficient as compared with methods employed in most other parts of the country, they could have been much better, and rehabilitation is possible. This conclusion may be challenged by oystermen, for the studies on which it is based did not consider adequately the economics of oyster planting.

The second most important food fish of the early days was the shad, entirely a wild crop. This fishery has declined just as sharply as the oyster fishery, and the causes are entirely by man: deterioration of the environment in the rivers where spawning takes place and the young live their early lives, overfishing, and lack of effective management measures. The decline of the menhaden industry also can be attributed to overfishing, but in this case in areas to the south, not under the control of the State of New York.

The prospect is bleak. The history of the fisheries of New York, as in so many other coastal States, is a history of mismanagement, or perhaps more accurately a classic example of no effective management at all. As in other coastal States, there has been no dearth of attention to the matter by the public and by government. The laws of New York State include many limitations upon fishing and upon degradation of the aquatic environment, but the history of the fisheries does not attest that these laws have been effective. Perhaps the best that can be said is that if there had been no laws, the decline probably would have been more rapid and more severe.

Two solutions to these problems are popular today. The first begins with the premise that all the problems of the domestic commercial fisheries are caused by foreign fishermen. The proposed solution is that the United States should assume ownership, or at least trusteeship, over the fishery resources of the continental shelf by extending its zone of jurisdiction unilaterally to 200 miles, as several Latin American countries have done. It is argued that the matter is urgent and that we cannot afford to wait for international action at the Law of the Sea Conference in 1973. Supporters of this view, who include most, if not all, people in the fishing industry on the Atlantic coast, believe that nothing useful to them is likely to emerge from the 1973 conference, if indeed any agreement on fisheries is reached, or if the conference materializes at all. Meanwhile, if we take no action, they argue, the situation will deteriorate rapidly.

This argument is open to question for several reasons. Not the least of these is the sorry history of our own attempts to manage the living resources of coastal waters over which we have always had control. This has been demonstrated very clearly for the coastal waters of New York in the present paper, and the record of most of our maritime States is equally bad. Only when we have been compelled to do so under international agreements, as in the salmon fisheries of the Pacific coast, has the United States succeeded in managing any major coastal fishery. If we move unilaterally to extend our fishery jurisdiction, there is nothing in the record to demonstrate that this will amount to anything but a hunting license to destroy the living resources of a much broader zone of the sea.

The second popular solution arises out of the long standing controversy between recreational and commercial fishermen. Most saltwater sport fishermen probably would support a move to extend the width of the fishery zone. In addition, they would welcome restrictions of various kinds on domestic commercial fishermen, on the grounds that the commercial fisheries take large quantities of fish which are more valuable as recreational resources, or that commercial fishermen destroy the food supply or the spawning grounds of recreational species. These tend to be emotional issues in which facts are ignored or distorted and uninformed opinions prevail. Where the sport catch has been demonstrated to exceed the commercial catch greatly, as is apparently true for species like bluefish and striped bass, the question arises whether sport fishing is not more in need of regulation than commercial fishing. The growing sport fisheries are under much less control than the commercial fisheries are, but from a scientific point of view they are equally in need of control if management is to succeed.

SOME QUESTIONS FOR CONSIDERATION

This preliminary study will be the first step in developing a marine fishery program in the State University of New York. The program will be developed in coordination with plans and programs of appropriate State and Federal agencies and other institutions concerned, to complement rather than to duplicate. The university has valuable skills and facilities for investigating aspects of the fisheries that government is not investigating or cannot do. Some of the questions are:

1. Which living resources are amenable to management by the State; and which are not, without cooperation from others?
2. What are the potential benefits of investing public funds in fishery research and management? Are they being realized now? Are they worth pursuing? What should be the priorities?
3. What are the present and potential economic values of marine commercial and recreational fisheries in the State? On what basis should the resources be allocated among users?
4. Can the present alarming trends in the marine fisheries of the State be arrested, and the fisheries stabilized for maximum (or optimum) yield? What will it cost? What benefits will accrue?
5. Does marine aquaculture hold promise for the economy of the State? In what ways? What are the priorities?
6. How can the university best use its capabilities for public education and extension services to create an enlightened constituency for utilization and management of the living resources of the sea?
7. What is the policy of the State toward fishery research, development, and management? Is it a rational policy? Is it working? If not, what should the policy be and how should it be implemented?

These are but a few of the questions that need to be answered, and which the State University is well qualified to answer. They will require the attention of many disciplines, including economics, sociology, government, law, and international affairs, as well as the natural sciences. This historical review has helped to phrase the questions, but it has answered few. It is just the beginning.

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SPACE SCALES OF SEA-SURFACE TEMPERATURE PATTERNS AND THEIR CAUSES

JEROME NAMIAS[1]

ABSTRACT

The space scales of monthly mean sea-surface-temperature (SST) anomalies over the North Pacific are determined from data gathered over a 20-year period and analyzed with the help of correlation fields. The characteristic scales are ascribed to complex coupling between the atmosphere and ocean—specifically to long waves in the upper westerlies and latitudinal variations in the westerlies, both of which produce anomalous oceanic advection and heat exchange. The coherence of mid-tropospheric (700-mb) heights, the cross-correlations between these and SST values, plus atmospheric "teleconnections" (long distance relationships) implicit in these upper-level flow patterns reveal the character of coupling.

At the historic 1958 CalCOFI meetings at Rancho Santa Fe the central theme was the large-scale climatic warming of the North and equatorial Pacific which had evolved over a few years preceding the conference (Sette and Isaacs, 1960). Elton Sette, who co-chaired this meeting, stimulated much discussion of the time and space scales of this warming. In his work over subsequent years he has made numerous major contributions to the subject of large-scale oceanic temperature patterns. It is the purpose of this note to bring to light some new data and ideas relevant to these problems and thus serve both as a testimonial to Elton's work and as an expression of gratitude for his unceasing encouragement to those of us working along similar lines.

The source of data for the present work is a series of monthly mean sea-surface temperatures (SST) extending from 1947 to 1966 generated at the Scripps Institution of Oceanography from files of about 8,000,000 ship reports which were compiled by the National Marine Fisheries Service from the National Weather Service reports. Monthly averages of 2° geographic squares were computed and then further averaged around 5° intersections for areas north of lat 20°N. A 20-year average for each month was then computed. Departures of the monthly means from the 20-year averages were used in the work described below along with 700-mb heights obtained directly from the National Weather Service.

To determine the coherence of North Pacific SST patterns and possible teleconnections between them I have correlated the SST deviations from the 20-year mean at one point with deviations of the other 154 points used in the 5° oceanic grid for each of the winter months (December, January, and February) over the 20-year period making a set of 60 values for each point. Examples are shown in the middle charts of Figures 1, 2, and 3. A similar procedure was used with the atmospheric 700-mb heights as shown in the upper charts of these figures. Finally, cross-correlation fields were prepared relating SST point values to the 700 mb-height values elsewhere as shown in the lower charts. The latter two sets of charts involving atmospheric parameters were constructed to help explain the physical nature of the large-scale air-sea coupling which accounts for the observed scale of the predominant SST patterns.

Before discussing these charts, I should mention that the 700-mb level rather than sea level

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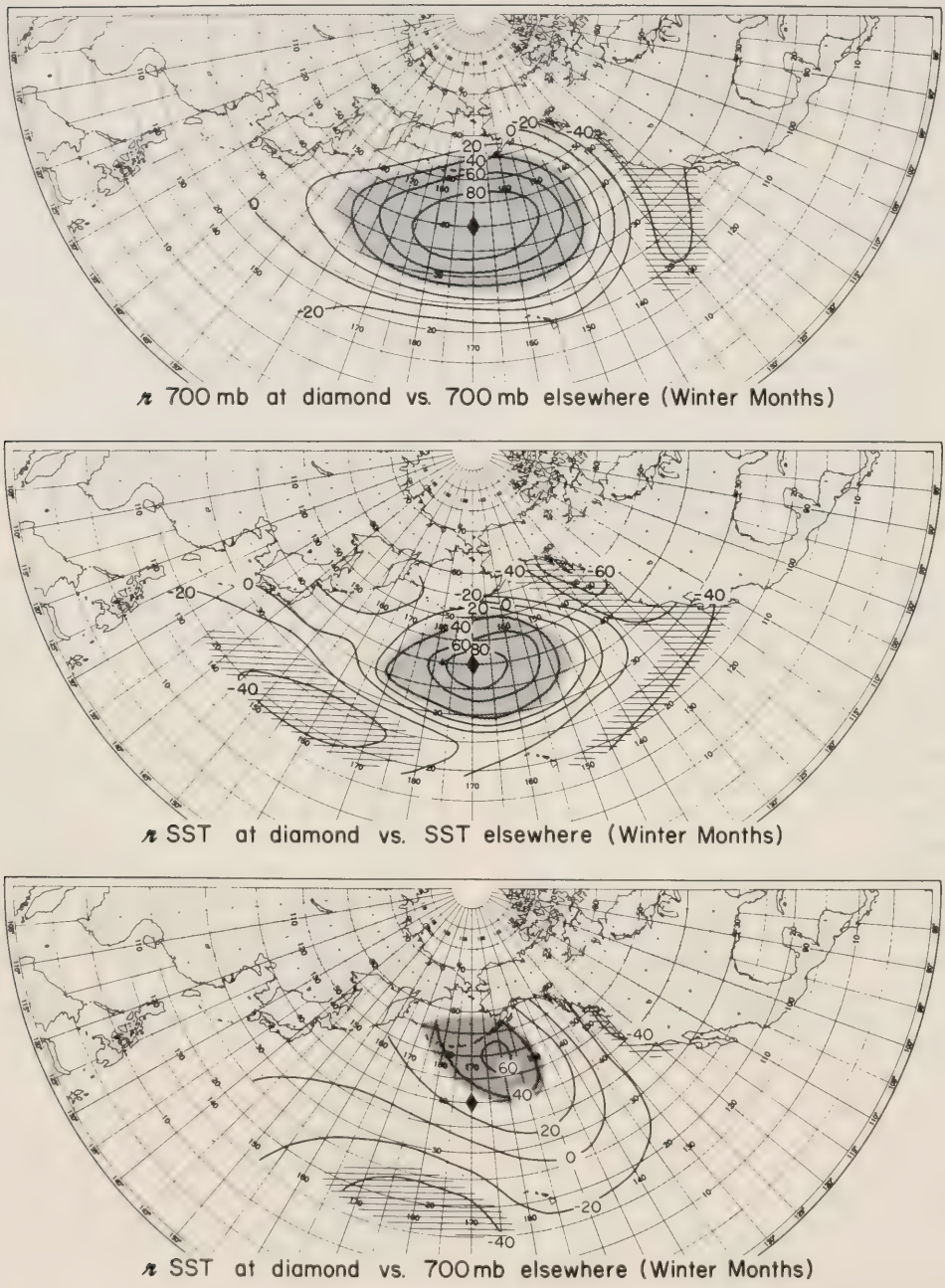

FIGURE 1.—Contemporaneous correlations between lat 40°N, long 170°W (diamond) and elsewhere for 700-mb heights (upper), sea-surface temperatures (middle), and SST vs. 700-mb (lower). Shaded areas represent correlations exceeding 1% level of significance—positive correlations stippled, negative hatched.

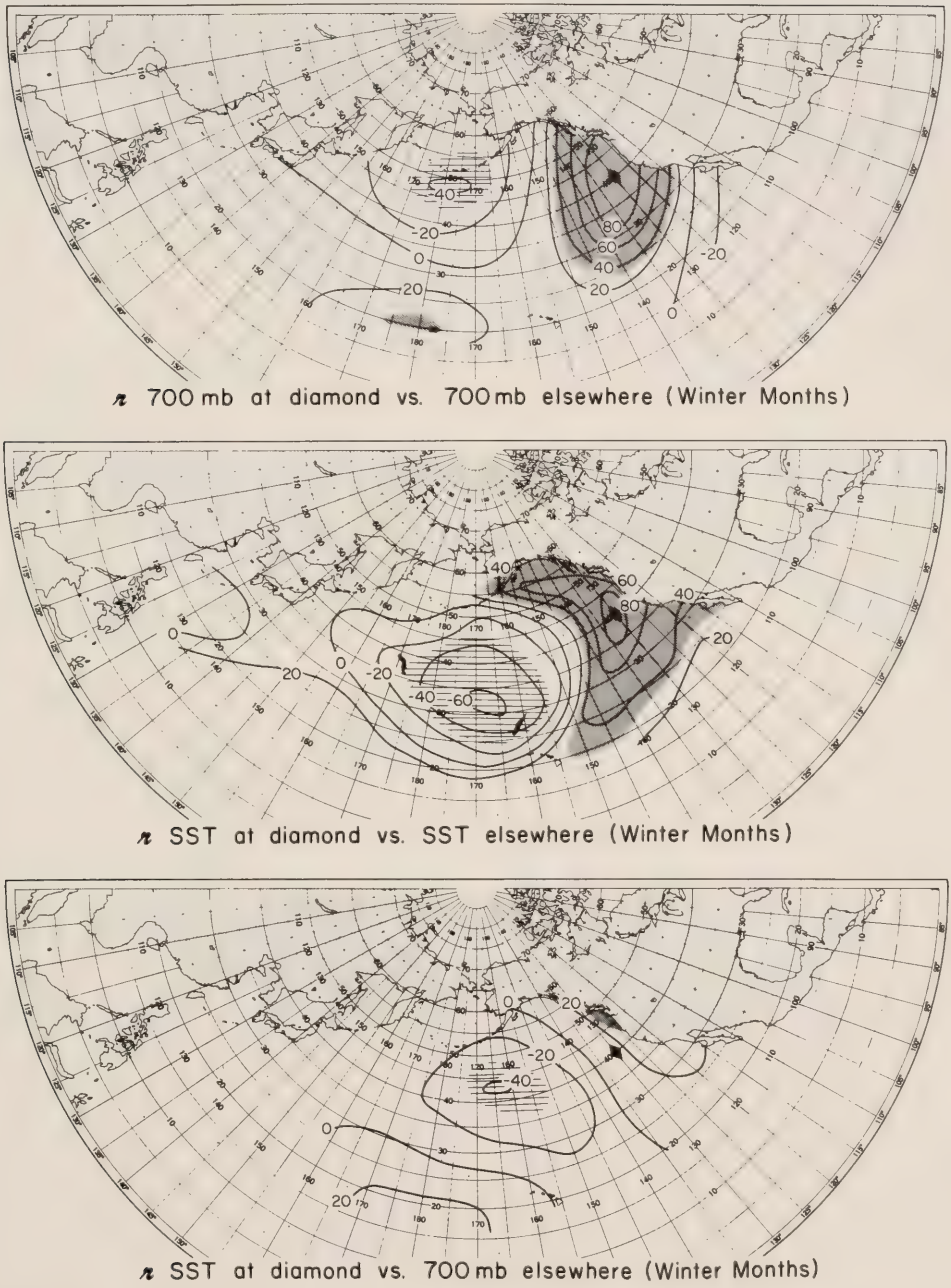

FIGURE 2.—Contemporaneous correlations between lat 40°N, long 130°W (diamond) and elsewhere for 700-mb heights (upper), sea-surface temperatures (middle), and SST vs. 700-mb (lower). Shaded areas represent correlations exceeding 1% level of significance—positive correlations stippled, negative hatched.

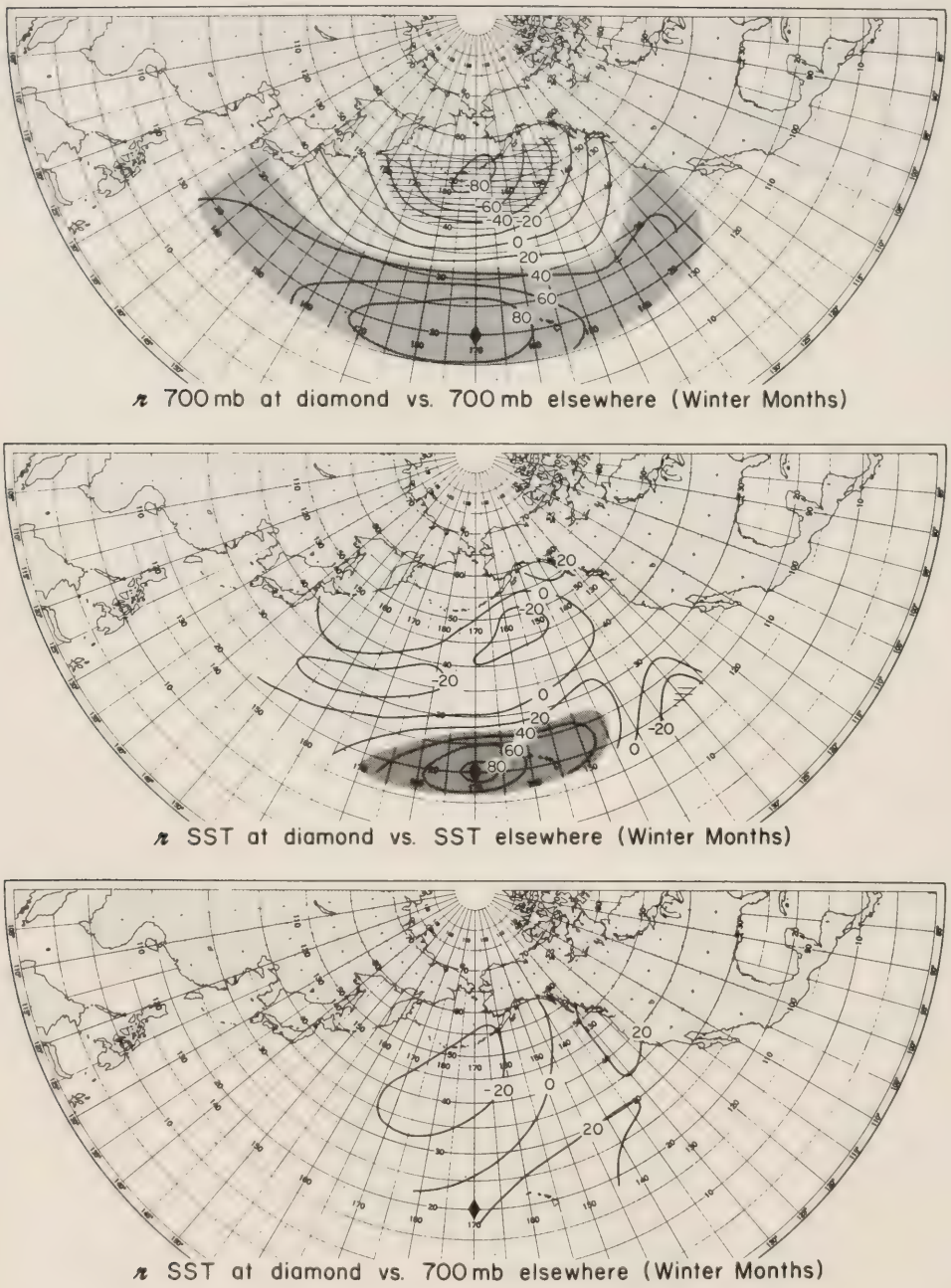

FIGURE 3.—Contemporaneous correlations between lat 20°N, long 170°W (diamond) and elsewhere for 700-mb heights (upper), sea-surface temperatures (middle), and SST vs. 700-mb (lower). Shaded areas represent correlations exceeding 1% level of significance—positive correlations stippled, negative hatched.

was chosen for the atmospheric variable because mid-tropospheric wind patterns often give a better specification of contemporaneous SST patterns than do sea-level maps. In general terms the physical reasons underlying this better specification from 700-mb rather than sea-level patterns lie in the fact that the 700-mb anomalies reflect not only the character of the anomalous sea-level pressure and wind distribution but they also contain implicitly the vertical stability of the lower troposphere. This association results from the high positive correlation between 700-mb height and mid-tropospheric temperature, and with cyclonic or anticyclonic contour curvature (Namias, 1947). The stability of the 1,000-700-mb layer to a large extent determines the vertical heat, moisture, and momentum flux from the surface—fluxes which are naturally important factors entering into the heat budget of the sea. Furthermore, since 700-mb height usually implies 700-mb temperature over ocean areas, some rough measure of back radiation is implied by the 700-mb heights.

Returning now to Figures 1-3 several points clearly emerge:

1. The space scale of coherent SST anomaly patterns is large—perhaps of the order of one-fourth to one-third of the North Pacific.

2. The SST scales are not far different from the 700-mb height scales and indeed display a remarkably similar form.

3. Strong teleconnections exist between SST anomaly fields of opposite sign over areas spanning almost one-half of the North Pacific; these teleconnections appear to be related to similar 700-mb teleconnections.

To aid the explanation of the above three empirical findings it should be remembered that time-averaged atmospheric patterns over large areas in temperate latitudes always reveal the presence of long or planetary waves whose horizontal dimensions are about 4,000 miles from crest to crest, but whose geographical positioning varies from month to month and also between the same month of different years. Thus, the atmospheric anomalies (and resultant prevailing winds and air masses) also vary. A quasi-stationary anomalous wind pattern generally creates anomalous SST patterns of a certain form. Most often cold water is advected and appreciable heat extracted in the cold dry northerly air currents behind mid-tropospheric troughs, while warmer water masses are advected and less heat extracted in the warm moist air currents ahead of troughs. Therefore, with atmospheric long-wave dimensions such as 4,000 miles (crest-to-crest) it is not surprising to find in Figure 1 that both 700-mb heights and SST anomalies are *negatively* correlated between the Central Pacific and the West Coast of the United States (one-half wave length) while both have similar coherence fields around the diamond.

Further clarification of the physical mechanism for this coupling can be obtained from the cross-correlations of SST with 700-mb height (Figure 1, lower). With anomalously warm water in the Central Pacific there are apt to be high 700-mb heights (anticyclonic ridge) in the north but low heights (cyclonic trough) in the south. Since correlation fields of the type shown in the upper and lower portions of Figures 1 and 3 may be interpreted in terms of flow (Stidd, 1954), we can approximate the resultant wind by remembering that it flows parallel to the contours with lower heights to the left. The anomalous wind component at the diamond is thus southeasterly and leads to less loss of heat by evaporation and sensible heat and greater advection of warm water from the south. Note also the contemporary reaction to *northerly* anomalous wind components in the eastern North Pacific—accounting for the colder than normal waters usually found there when the diamond area is warm. Of course, the above reasoning may also be applied (in reverse sense) when anomalously cold water exists at the diamond.

Figure 2, relating surrounding values to the diamond at lat 40°N, long 130°W, also shows the large-scale coherence and area of negative correlation one-half wave length upstream. The isopleths in the bottom figure indicate warm southerly air flow and warm sea transport accompanying positive SST values at the diamond and negative 700-mb height departures from normal in the Central Pacific. Of course, abnormally low SST values at the diamond imply

anomalous cold air and sea advection from the north.

Figure 3, which relates surrounding values to the diamond at lat 20°N, long 170°W, instead of demonstrating the east-west (trough-ridge) teleconnections described in connection with Figures 1 and 2, focuses on north-south teleconnections. These relationships were first pointed out by Walker and Bliss (1930) in studies of the North Pacific Oscillation, and later expanded by Willett, Bodurtha, and staff (1949),[2] Lorenz (1951), and O'Connor (1969). The upper section of Figure 2 shows that 700-mb heights are strongly negatively correlated between lat 20°N and 50°N, implying a north-south half-wave length of some 30° latitude.

A large part of this negative correlation is associated with "blocking" situations (low zonal index patterns) wherein anticyclones are found near the Aleutians contemporaneously with cyclones near Hawaii (Kona Storms). In the reverse case, abnormally strong Aleutian Lows are usually accompanied by strong subtropic anticyclones (high zonal index patterns).

The middle portion of Figure 3, while showing large-scale coherence around the diamond, indicates that the area of negative correlation lies farther south in the SST pattern than in the 700-mb pattern, so that little correlation exists between SST anomalies at lat 50°N and lat 20°N in the central North Pacific. Probably this small degree of correlation implies a much more complex mechanism than wind-driven advection and heat exchange, or that sea-level anomalies in these situations are not well prescribed by the 700-mb anomalies. Also, the diamond lies outside the zone of major influence of the westerlies.

Although there is a strong tendency for North Pacific SST anomaly patterns to have compensating large pools of warm and cold water, it should not be assumed that the mean temperature anomaly of the entire North Pacific is zero. Figure 4 shows that the mean SST for the entire

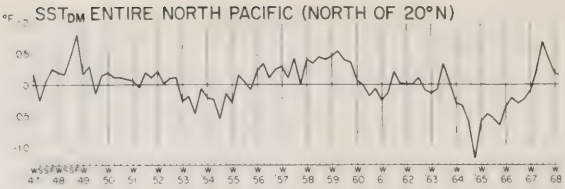

FIGURE 4.—Departures of mean sea-surface temperature (°F) from the 1947-66 averages over the entire North Pacific, north of lat 20°N.

North Pacific (north of lat 20°N) varies over a range of about 2°F in extreme seasons, and as much as 1°F in extreme *years*! Assuming normal atmospheric parameters, a 1°F change would imply a difference in heat of evaporation of 47.8 $\times 10^{20}$ cal., equivalent to the evaporation of 8.14 $\times 10^{18}$ g of water or about 23.4 cm of water over the entire North Pacific. The oceanic mean SST anomalies are highly correlated with the area occupied by positive signs of the SST anomalies ($r = 0.84$). Thus, the North Pacific mean anomaly is often determined not by the domination of some extreme values but by the vast extent of major anomalous areas. For example, during the extreme negative SST anomaly of fall 1964 and extreme positive anomaly of summer 1967 (see Figure 4) 14% and 73% respectively of the North Pacific had positive signs. Large areal anomalies of this sort arise from the fact that the sea has a much greater persistence than the atmosphere (Namias and Born, 1970). Hence, large warm or cold pools in one area, such as the western Pacific, are apt to resist rapid change over a month or even a season, while the eastern Pacific may be undergoing more rapid response. This differential rate of response may be due to a more shallow thermocline in one area of the Pacific than another and/or more vigorous atmospheric circulation changes.

These almost ocean-wide extremes of SST are naturally transitory, because their space scale is not compatible with modal long-wave atmospheric patterns, so that ultimately compatible patterns must be restored.

The high positive correlation between mean SST over the entire North Pacific and percent of the total area occupied by positive signs may

[2] Willett, H. C., F. T. Bodurtha, and Staff. 1949. Final report of the Weather Bureau - M.I.T. extended forecasting project for the fiscal year July 1, 1948-June 30, 1949. Mass. Inst. Technol., Cambridge, Mass., 109 p. ("Memorandum of Understanding" with the U.S. Weather Bureau.) [Processed.]

TABLE 1.—Correlation relating mean SST over North Pacific (north of lat 20°N) and percent of positive signs of anomalies at 5° squares (based on 21 years of data), and standard deviations of these quantities.

	Correlation $\overline{SST}$ vs. % positive anomalies	σ $\overline{SST}$ (°F)	σ % of positive signs
Winter	0.83	0.28	9.77
Spring	0.71	0.25	9.20
Summer	0.87	0.37	14.18
Fall	0.86	0.40	14.21
All seasons (overall)	0.84	0.32	11.90

be found in all seasons with only small differences (see Table 1). However, the variability in percent of similar signs and mean SST seems to be seasonally dependent with summer and fall having greater variability than winter and spring, as shown by the standard deviations of SST and percent of positive signs listed in Table 1. In the warm season small changes in cloud cover and wind can produce large changes in SST since only a thin wind-mixed layer is affected. These changes often extend over vast areas because of variations in the great Pacific High and peripheral storm tracks.

ACKNOWLEDGMENTS

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MONTHLY SEA LEVEL DIFFERENCES BETWEEN THE HAWAIIAN ISLANDS AND THE CALIFORNIA COAST

J. F. T. Saur[1]

ABSTRACT

Time series of monthly sea level differences, adjusted for linear trends and the isostatic effect of atmospheric pressure, are computed for Honolulu-minus-San Francisco (1905-69) and Hilo-minus-Avila (1947-59 and 1961-67) as an index to broad scale changes in current around the eastern limb of the North Pacific anticyclonic current gyre.

The normal seasonal cycle of sea level differences imply a net southeastward surface current that is strongest from April through October and weakest from December through February and the range is about 20% of the average. Nonseasonal differences for Honolulu-minus-San Francisco and Hilo-minus-Avila show a highly significant correlation over the 240 months of coincident records. Inferences regarding nonseasonal large-scale long-term changes in geostrophic current are drawn from the 65-year Honolulu-minus-San Francisco smoothed monthly anomalies in which variability of less than 6 months was suppressed, as follows: 1) nonseasonal changes in current speed exceed $\pm$ 10% of the normal current over one-third of the time and range up to 54% of the normal monthly current, 2) the periods 1922-38 and 1950-54 were eras of low variability as compared with greater variability in the rest of the record, and 3) periods of weakest circulation were in 1911, 1918, 1941, 1957-58, and 1967, and of strongest circulation in 1915, 1920-21, 1943-44, 1948-49, and 1959.

For more than a decade there has been a rapidly growing interest of fishery scientists and biological oceanographers in the role of the environment in fishery problems. One objective is to include environmental effects in models of population dynamics and in fishery forecasting procedures. However, to do this, environmental characteristics which are significant to fisheries must be determined and set forth in quantitative form. One empirical approach to these complex environmental problems is to compile historical oceanic and atmospheric data into time series to gain a knowledge of the mean seasonal cycles and variability, identify periods of highly anomalous environmental conditions for further study, and seek an understanding of cause-effect relations which bring about the observed changes. Such an understanding would be useful for efficient monitoring of the oceanic environment and in predicting environmental conditions.

Oceanographic data with good time and space distribution for time-series studies of environmental changes of a few months to several years are woefully scarce. Only sea-surface temperature observations taken by ships as a part of the marine weather observations have long-term continuity in time as well as oceanwide distribution. As a result, these have been used extensively in air-sea interaction studies and to indicate oceanic changes.

To augment the sea temperature data, mean sea levels compiled from continuous tidal records at coastal and island stations provide another source of long time-series data on ocean variability. The statistical characteristics and interrelations of the sea levels, atmospheric pressure, and temperature of many coastal and island stations in the Pacific have been described in several papers by Roden (1960, 1963, 1966) using autocorrelation, spectral, and coherence techniques.

[1] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

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The data have been less utilized in the study of specific oceanographic changes. Stewart, Zetler, and Taylor (1958) pointed out the rise in sea level along the west coast of North America during the warming period of 1957-58. Bjerknes (1966) also noted changes in sea levels along the equator during El Niño, i.e., warming which occurs off the Pacific coast of South America, during the same 1957-58 period.

In this paper the use of sea level information in the northeast Pacific Ocean to augment inferences about oceanographic changes is explored. The geostrophic equation requires that the speed of the surface current be proportional to the transverse slope of the sea surface. Thus time series of differences in sea level between the Hawaiian Islands and the California coast could be an index to broad-scale changes in surface current in the eastern North Pacific Ocean. Some earlier exploratory work on sea level differences between Honolulu and San Francisco through 1962 was reported orally at meetings of the American Geophysical Union (Saur, 1966). These preliminary results indicated that a pronounced weakening of the strength of the south flowing current around the eastern limb of the North Pacific current gyre was associated with the warm winters of 1940-41 and 1957-58, which have been reported for the California Current region (Reid, 1960; Robinson, 1961). The occurrence of El Niño in these same periods (Bjerknes, 1961, 1966) further indicated the possibility of a relaxation in strength of ocean current systems in the eastern Pacific on a broad scale.

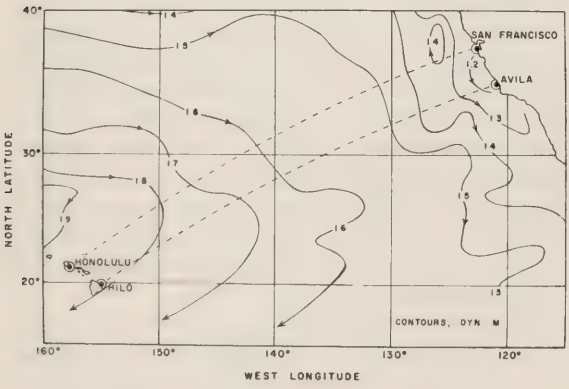


FIGURE 1.—Station locations and general pattern of surface currents (solid contours: geopotential anomaly at the sea surface relative to the 1,000 db surface, in dynamic meters) after the NORPAC Atlas (Oceanic Observations of the Pacific, 1960) but modified near the Hawaiian Islands per Reid (1961) and Seckel (1962). Dashed lines are great circles joining pairs of tide stations for which sea level differences are calculated.

No time series of direct observations of ocean conditions exist to study such broad-scale changes in current, and certainly not of the continuous nature of sea level data. In this paper therefore, the normal seasonal cycles of sea level differences between the Hawaiian Islands and the California coast are presented and some inferences are drawn from the 65-year record of Honolulu-minus-San Francisco differences about the character of changes of surface current in the region.

EARLIER STUDIES

Montgomery (1938) was the first to use the cross-current difference in sea level in the geostrophic equation to estimate the range of fluctuation of ocean current. Using changes in sea level difference between Charleston, S.C., and Bermuda, he found the range of seasonal variation was about 32% of the average difference. Stommel (1953) used fluctuations in cross-current sea level differences between Havana and Key West and between Cat Key and Miami as a measure of current in developing a model of the structure of the Florida Current. More recently, Wunsch, Hansen, and Zetler (1969) measured statistical variability of the Florida Current by spectral and coherence analyses of longer sea level records at the same four stations. They found that the apparent seasonal variation of the Florida Current accounts for only about 10% of the root-mean-square modulations for periods from 2 days to 1 year. They further concluded that monthly mean sea levels could be used to indicate long-period fluctuations.

Changes in mean sea levels at shore stations have been favorably compared by other investigators with changes in geopotential height of the sea surface in deep water offshore as traditionally determined from observed subsurface distribution of density of the water column. Mont-

gomery (1938) cautioned that he had only a meager number of hydrographic stations for this, but other studies since that time tended to confirm his results.

For the southern California coast, LaFond (1939) found good agreement between weekly sea level and contours of dynamic height (0/500 db) extrapolated to the tide station. Special observations of sea level and temperature structure were carried out at many island stations during the International Geophysical Year from which Lisitzin and Pattullo (1961) concluded that in the open ocean most of the deviations from mean sea level can be explained by combined atmospheric pressure effects and steric effects, the latter being defined as those due to changes in the specific volume of the water column, i.e., those measured by dynamic height anomalies. Shaw and Donn (1964) had 173 hydrographic stations, taken approximately biweekly by the *Panulirus* off Bermuda over a period of nearly 7½ years, to compute steric levels for comparison with sea levels. They found that about 80% of the variance of raw sea levels, which included the seasonal cycle, resulted from a combination of the atmospheric pressure effect, which was weak, and the steric effect, which was dominant.

Sturges (1966) has shown high correlations between steric levels and mean sea level at two Pacific coast locations. The least squares regression of steric levels computed for the coast against 3-day sea level (adjusted for atmospheric pressure) for Neah Bay, Wash., was 0.97 with a standard error of estimate of 4.1 cm and a correlation of 0.904. The regression coefficient at San Diego, Calif., was only 0.61 with a standard error of estimate of 2.2 cm and a correlation of 0.914. Theoretically, for variations of sea level adjusted for pressure to agree with steric level, the slope of the regression should be unity. Sturges also estimated the wind set-up effect at Neah Bay, which has a narrow continental shelf, to be negligible.

Such studies indicate, as summarized by Donn, Pattullo, and Shaw (1964), that the combined atmospheric pressure and steric effects account for most of the sea level variations of periods longer than a few months. Thus, the interpretations made here assume that sea level differences, suitably adjusted for trends and atmospheric pressure, are a reasonable measure of changes in broad-scale geostrophic currents.

SURFACE CURRENTS OF THE REGION

Our area of interest is shown in Figure 1. Sea level differences between Honolulu and San Francisco and between Hilo and Avila are to be studied. The great circles joining each pair of stations span the same region of the eastern North Pacific Ocean.

The currents in the region are part of the eastern limb of the major anticyclonic current gyre of the North Pacific Ocean. The general pattern is shown in Figure 1 by the 0/1,000 db contours of dynamic height anomaly. The surface current is generally to the southeast, nearly normal to the great circles over most of the distance. At these latitudes the California Current extends from the California coast to about long 130°W, or somewhat farther, and about one-half of the change in geopotential anomaly takes place across this current, i.e., in less than one-third the distance between the stations. As a typical eastern boundary current (Wooster and Reid, 1963), it is broad, sluggish, and reinforced by coastal upwelling during the spring and summer months. During the winter months, December through February, a narrow north flowing countercurrent, often referred to as the Davidson Current, frequently occurs at the surface along the central California coast.

The California Current feeds into the North Equatorial Current, the axis of which lies south of lat 20°N (Seckel, 1962) so that there is generally a southward component across the great circle near the Hawaiian Islands. Occasionally, however, there is a west-northwestward flow along the east side of the islands, as evidently occurred at the time of the 1955 Norpac survey (Oceanic Observations of the Pacific, 1960). Corresponding to this return flow across the great circle, the sea levels at the Hawaiian stations would be lower than sea level northeast of the islands. Such localized conditions cannot be revealed by the sea level data, and thus are one source of "noise" in the data.

DATA AND PROCEDURES

Monthly mean sea levels were obtained from the National Ocean Survey[2] which has for many years compiled these data for its tide stations. The coincident period of record for Honolulu and San Francisco is 65 years, 1905-69. The coincident period for Hilo and Avila is 20 years, 1947-59 and 1961-67. It is broken and shortened because of incomplete records at Avila. However, Avila was selected among other California stations to pair with Hilo, so that the great circle between them would be close to that joining Honolulu and San Francisco and would cross essentially the same currents.

All of the tide gauges have moderately good exposure. Hilo and Avila are small coastal harbors protected by artificial breakwaters. The Honolulu gauge is in the outer of two harbor areas just inside of the entrance channel. The San Francisco gauge is at Fort Point just below the Golden Gate Bridge on the south side of the entrance to San Francisco Bay. Depths of 100 fm (183 m) are less than 10 km offshore from Hilo and Honolulu tide gauges, less than 20 km off Avila, and about 55 km off San Francisco.

ELIMINATION OF TRENDS

The sea level observations refer to the level of the ocean surface relative to the adjacent land. The annual mean sea levels at each of the four stations increase irregularly with time as shown in Figure 2. Such long-term trends as are due to a combination of change in the total mass of ocean water by melting (or accretion) of glaciers and of local subsidence (or emergence) of the land on which the gauge is located (Hicks and Shofnos, 1965), need to be eliminated from the data.

The linear trends determined by least squares regression, of 0.17 cm/year at Honolulu and 0.20 cm/year at San Francisco (Figure 2) are essentially the same as reported by Hicks and Shofnos (1965) for sea levels through 1962 at the same stations. The trend of 0.24 cm/year at Avila is only slightly larger than the first two, but the trend of 0.57 cm/year at Hilo is well over twice as large. In a computer analysis of the tide records at five stations in the Hawaiian Islands, Moore (1971) found a pattern of near zero trend at the older islands to the northwest increasing consistently toward the southeastern younger islands. Moore attributes the greater trend at Hilo to subsidence caused by loading of the crust by active volcanism. An interesting study by Apple and MacDonald (1966) of archeological features—native bait cups, net tanning tubs, and playing boards—carved into a newly submerged reef at Honaunau, Hawaii, further indicates a century of subsidence like that indicated by the recent tide gauge records.

By an indirect method using the decay constant of the autocorrelation coefficient Roden (1966) examined the consistency of trends for moving 30-year periods in the longer records at Honolulu and San Francisco. He found that the 30-year trends at Honolulu varied irregularly from 0.12 cm/year to 0.25 cm/year. At San Francisco the trends were low (about 0.05 cm/year) for the 1904-35 period, rising gradually and leveling off at about 0.25 cm/year for 30-year periods starting after 1915. Since not enough is known about the possible meteorological and oceanographic contributions to these trends, only the long-term linear trends shown in Figure 2 have been eliminated.

ADJUSTMENT FOR ATMOSPHERIC PRESSURE

There is general agreement that for periods of 1 month or more the ocean maintains an isostatic equilibrium with changes in atmospheric pressure. Assuming the average pressure over the whole ocean to be constant, if the pressure difference between two locations changes, the elevation of the sea surface changes in a compensatory manner so that there is no change in distribution of pressure on the sea floor. There is no balancing current associated with this portion of the slope of the sea surface which is balanced by the atmospheric pressure gradient. There-

[2] Formerly the Coast and Geodetic Survey, Environmental Science Services Administration.

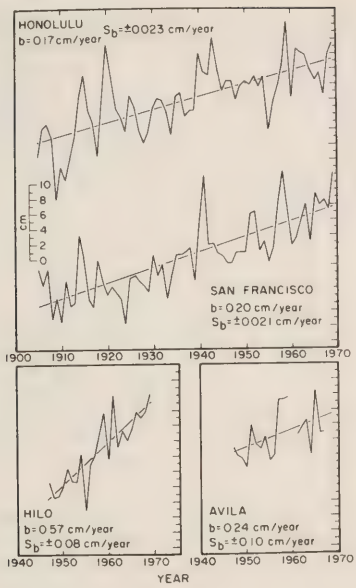


FIGURE 2.—Changes in annual mean sea level at four tide stations and linear trends determined by least squares regression. Slope of regression, b, and standard error of regression, s_b, are shown.

fore, an adjustment for this "inverted barometer" effect is made by correcting the sea levels to a "normal" atmospheric pressure which compensates for both the normal seasonal cycle and the monthly anomaly of atmospheric pressure at the station. For our purpose a correction of 1 cm in sea level for 1 mb change in atmospheric pressure is sufficiently accurate. Adjustments of less than 1 cm for monthly deviations of mean atmospheric pressure over the world oceans reported by Pattullo et al. (1955) have not been made to the individual station data reported here, because they are small and would have no effect on sea level differences.

Monthly mean atmospheric pressure reduced to sea level from weather observations of the National Weather Service at Honolulu, San Francisco, Hilo, and Santa Maria (less than 20 nautical miles from Avila) were obtained mainly from published sources. The World Weather Record series (Clayton, 1944a, 1944b; Clayton and Clayton, 1947; U.S. Weather Bureau, 1959, 1965, 1968) contain climatological data, including monthly atmospheric pressure, through 1960. Monthly mean pressures for first order weather stations are included in the monthly issues of Climatological Data, National Summary, U.S. Environmental Data Service, published since January 1950. Some manuscript records obtained directly from the Weather Service offices were helpful in standardizing all pressure data to sea level.

NORMAL SEASONAL CYCLES OF SEA LEVEL AND SEA LEVEL DIFFERENCE

The *normal* monthly sea levels are obtained by averaging the monthly sea levels[3] for a given month from all years of record. Because the zero level for the scale on the tide gauge is arbitrary at each station the normal monthly sea levels are shown in Table 1 in terms of departure from the long-term mean for all months and years. The standard deviations for given months in Table 1 are measures of the year-to-year variability of monthly sea level for the given month. From these one can compute that the 95% confidence limits on the monthly normals for Honolulu and San Francisco are 0.8 cm or less, and 1.4 cm or less for Hilo and Avila.

We are interested in the real differences in normal monthly sea level between stations as a base against which to measure the variability. For continental stations it is possible to determine this difference of long-term mean sea level between two stations by reference to the geodetic leveling network,[4] but no such reference leveling exists between the continent and Hawaiian Islands. As described in the next section, the long-term sea level difference has been estimated using oceanographic data.

COMPUTATION OF LONG-TERM MEAN SEA LEVEL DIFFERENCE

The long-term mean sea level differences between Honolulu and San Francisco and between

[3] Monthly sea level with trend removed and adjusted to normal atmospheric pressure is hereafter implied.

[4] From oceanographic data, however, Sturges (1966) suggests there may be some systematic north-south leveling error.

TABLE 1.—Departures of normal monthly sea level, $\bar{h}$, from the long-term mean at each tide station; normal monthly sea level difference, $\bar{d}$; and standard deviations, s, of monthly values for total years of record, in centimeters. Honolulu and San Francisco, 1905-69; Hilo and Avila, 1947-59 and 1961-67.

Month	Honolulu		San Francisco		Honolulu-San Francisco		Hilo		Avila		Hilo-Avila	
	$\bar{h}$	s_h	$\bar{h}$	s_h	$\bar{d}$	s_d	$\bar{h}$	s_h	$\bar{h}$	s_h	$\bar{d}$	s_d
Jan.	−1.9	4.4	5.4	5.3	50.6	6.9	−2.0	4.2	4.6	4.4	46.0	4.2
Feb.	−1.7	4.4	4.4	6.3	51.9	6.8	−3.1	3.7	1.1	4.3	47.6	4.4
Mar.	−1.7	5.1	−1.1	6.0	57.4	7.6	−2.9	5.1	−4.6	3.8	53.3	6.3
Apr.	−2.8	5.3	−5.1	4.6	60.3	7.2	−2.2	4.2	−6.9	3.5	56.6	6.0
May	−2.6	5.1	−6.3	3.4	61.7	5.8	−3.3	5.3	−6.6	3.6	55.7	5.6
June	−2.0	5.6	−4.6	2.6	60.6	6.3	−2.5	5.9	−4.3	2.9	53.9	6.0
July	0.3	5.8	−1.3	2.8	59.6	6.4	0.9	5.0	0.0	3.6	53.3	5.2
Aug.	2.6	5.5	−0.5	2.8	61.1	5.8	4.0	4.6	2.2	3.6	53.9	4.7
Sept.	3.7	4.7	1.0	3.2	60.8	5.7	4.4	4.7	3.2	3.7	53.1	6.4
Oct.	3.7	4.7	1.0	3.7	60.7	6.1	4.1	3.5	3.2	4.4	52.9	4.5
Nov.	2.1	3.9	2.3	4.4	57.8	5.8	2.8	4.3	3.8	3.7	50.6	4.8
Dec.	0.1	4.5	4.6	4.9	53.5	6.3	0.0	5.1	4.4	5.1	47.0	5.5

Note: Long-term mean differences, Honolulu-minus-San Francisco and Hilo-minus-Avila, have been adjusted to 58 cm and 52 cm, respectively, by reference to 0/1,000 db dynamic heights, as described in text.

Hilo and Avila have been estimated from 0/1,000 db dynamic height anomalies. Reed (1970) has shown that the real topography of the 1,000 db surface between Honolulu and San Francisco is probably 1 cm or less.

The dynamic height anomalies were obtained from listings of hydrographic station data supplied by the National Oceanographic Data Center and data reports of the Trade Wind Zone Oceanography (TWZO) Program (Charnell, Au, and Seckel, 1967a, b, c, d, e, f).

Information on the number of stations, location, and average dynamic height anomalies is given in Table 2. The locations of the hydrographic stations relative to the tide stations are shown in Figure 3. Frequent observations made since 1949 by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) made it possible to get a good sampling of stations very near the two California tide stations. The density of sampling was much lower near the Hawaiian Islands, so observations over broader geographic regions were used. The mean dynamic height anomalies were computed for several independent sets of observations in the vicinity of Honolulu and Hilo to reveal the extent of island effects, but no large differences were found in the averages.

All oceanographic stations were taken since 1947. Sampling of different months throughout the year was good. Long-term mean Honolulu-minus-San Francisco sea level difference was found to be 58 cm and the Hilo-minus-Avila difference was 52 cm. The normal monthly sea level differences in Table 1 reflect the adjustment of long-term mean sea level differences to these values.

HONOLULU-MINUS-SAN FRANCISCO

The seasonal variation of the normal monthly sea level difference for Honolulu-minus-San Francisco sea level difference is shown in the upper part of Figure 4. The cycle is asymmetric about the mean level. The monthly difference is high, forming a plateau, in the months from April through October, and a sharp minimum occurs from December through February. March and November are transitional months. The range of the normal seasonal cycle is 11 cm or 19% of the long-term mean difference of 58 cm.

The lower part of Figure 4 shows how the normal seasonal cycles at each station contribute to the seasonal cycle of the difference. The monthly normal at San Francisco is lowest in May, early in the upwelling season. The Honolulu sea level is also at its minimum, but the magnitude of the negative departure at San Francisco is more than double that at Honolulu and the normal cycle of sea level difference is at its maximum. Both station curves rise at nearly the same rate from June to October. A somewhat more rapid rise in July at San Francisco,

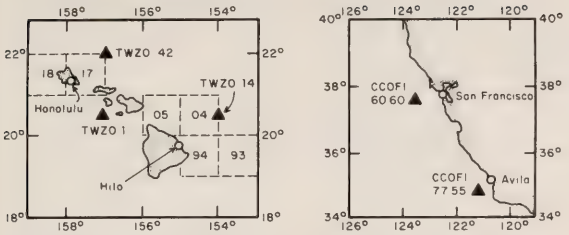


FIGURE 3.—Locations of hydrographic station data used to determine long-term differences in sea level as referred to in text and in Table 2. CCOFI = California Cooperative Oceanic Fisheries Investigations. TWZO = Trade Wind Zone Oceanography program. Two-digit numbers are 1-degree square (dashed lines) identification used in National Oceanographic Data Center listings of hydrographic station data.

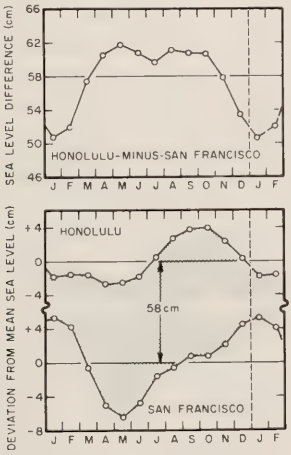


FIGURE 4.—Seasonal deviations of 65-year normal (1905-69) monthly sea levels (trend removed and adjusted to normal pressure) from long-term mean, Honolulu and San Francisco (below). Seasonal cycle of normal monthly sea level difference (above). Difference of long-term mean sea level of 58 cm was determined from hydrographic station data (see text).

probably due to heating, giving way to a more gradual rise into autumn, results in a slight dip during July in the plateau of the difference. The sea level at Honolulu drops rapidly from October to January. At San Francisco, however, the sea level continues to rise from November to its highest value in January. Some of this rise is undoubtedly the result of the frequent occurrence of the north-flowing coastal countercurrent in these months (Reid, Roden, and Wyllie, 1958), while some may be due to decrease in the speed of the south-flowing current offshore. The proportions cannot be determined from the sea level data. The combined changes at Honolulu and at San Francisco result in a sharp winter minimum in the normal cycle of sea level difference.

HILO-MINUS-AVILA

The seasonal variation of the normal monthly sea level difference for Hilo-minus-Avila (Figure 5) is similar to that for Honolulu-San Francisco. A winter minimum occurs in December-February, and the maximum occurs in the spring. However, after a decrease of a few centimeters to July the normal difference remains at a nearly constant level through October rather than rising again as it did for Honolulu-San Francisco. March and November are transitional months except that March has a normal difference as high as those for late summer. The range of the normal seasonal cycle

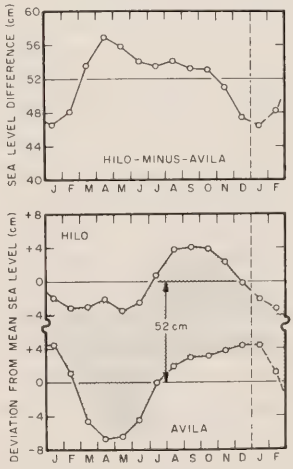


FIGURE 5.—Seasonal deviations of 20-year normal (1947-59, 1961-67) monthly sea level (trend removed and adjusted to normal pressure) from long-term mean, Hilo and Avila (below). Seasonal cycle of normal monthly sea level difference (above). Difference between long-term mean sea level of 52 cm was determined from hydrographic station data (see text).

is 10.6 cm, or 20% of the long-term mean sea level difference of 52 cm.

The seasonal cycle for Hilo is very much like that at Honolulu. The slight peak in April at Hilo, which does not occur at Honolulu, combined with the April minimum at Avila causes the maximum in the sea level difference to occur 1 month earlier for Hilo-Avila than for Honolulu-San Francisco. The normal seasonal cycle at Avila tends to lead that at San Francisco by 1 month. A stronger rise occurs at Avila in June-August than at San Francisco, which may be a heating effect because Avila is at a lower latitude.

DISCUSSION

The characteristics of the normal seasonal cycles of sea level difference for both pairs of stations are in agreement with each other and in accord with our knowledge from other sources of the oceanography of the northeast Pacific and California Current. The geostrophic equation requires that the speed of the surface current be proportional to the transverse slope of the sea surface. From the sea level difference we can infer that the average current normal to the great circles between the Hawaiian Islands and the California coast is southeastward throughout the year. It is strongest in the upwelling and summer season when the North Pacific atmospheric high pressure cell is best developed. It is weakest during the winter season.

Using an average latitude between stations and the long-term differences in the geostrophic equation, the average current to the southeast is 2.0 cm/sec for the Honolulu-San Francisco difference and 1.9 cm/sec for the Hilo-Avila difference. The range of the normal seasonal cycle, as noted earlier, is 20%.

It must be kept in mind that the sea level difference indicates only the average geostrophic surface current normal to the line between the two stations. For the California Current the contours of 0/500 db dynamic height anomaly in the CalCOFI Atlas No. 4, Geostrophic Flow (Wyllie, 1966) indicate that the speed averaged over a distance of 1,000 km is about 5 to 10 cm/sec, whereas there may be narrow regions about 100 km in width with current of 25 cm/sec, or greater.

COMPARISON OF MONTHLY SEA LEVELS WITH STERIC LEVELS

Monthly sea level differences are to be used to estimate the slope of the sea surface and draw inferences regarding month-to-month and year-to-year changes in current from the geostrophic equation. Traditionally the slope is estimated indirectly by computing geopotential heights, or steric levels. Therefore, the agreement between monthly sea levels and steric levels at nearby offshore locations was investigated using hydrographic station data, employed earlier to establish the long-term mean differences in sea level between pairs of stations. Correlation coefficients between the monthly sea levels, linearly interpolated to the date of each hydrographic station, and the steric levels are given in the last column of Table 2. For San Francisco and Avila, where a large number of hydrographic stations were made within a small area at nearby locations, the correlation coefficients are 0.54 and 0.57 respectively. Both coefficients are considerably higher than the 1% level of significance.

For Honolulu the correlations from four sets of data from different areas are quite consistent, ranging from 0.54 to 0.65. These coefficients are as large as those for San Francisco and Avila, but because of the smaller sample sizes are statistically significant only at the 5% level.

For Hilo the correlations for three different sets of steric levels are less consistent. A high correlation, $r = 0.78$, which is significant at the 1% level, was obtained with Hilo monthly sea levels only from the set of 10 steric levels from observations in 1-degree squares 04 and 05 immediately northeast of Hilo. Dynamic topography charts in TWZO data reports (Charnell et al., 1967a, b, c, d, e, f) reveal that the presence of an anticyclonic eddy or ridge northeast of Hilo at TWZO station 14 during 5 of the 16 observational periods caused the lower correlation of data from that station with Hilo sea levels. One suspects some similar local effect as

TABLE 2.—Determinations of long-term mean sea level differences from 0/1,000 db geopotential (steric) anomalies at nearby offshore locations. Correlations, r, of monthly sea levels with geopotential anomalies.

Shore station	Data source	Location of hydrographic stations (see Figure 3)	Distance from shore station (km)	No. of observations	Average steric anomaly, 0/1,000 db (dyn cm)	Correlation, r steric vs. sea level
Honolulu	NODC	1-degree square 17, Marsden square 088	10-100	10	[1] 182.4	0.65*
	NODC	1-degree square 18, Marsden square 088	30-120	12	[1] 182.2	0.64*
	TWZO	Station 1	100	16	184.3	0.60*
	TWZO	Station 42	120	15	184.0	0.54*
San Francisco	NODC	CalCOFI 60.60	105	52	[2] 125.2	0.54**
		Long-term mean sea level difference, Honolulu-minus-San Francisco = 58 cm				
Hilo	NODC	1-degree squares 04, 05, Marsden square 088	10-150	11	[1] 179.5	0.78**
	NODC	1-degree squares 93, 94; Marsden square 052	20-200	10	[1] 179.3	0.48
	TWZO	Station 14	140	16	181.1	0.42
Avila	NODC	CalCOFI 77.55	50	42	[3] 127.5	0.57**
		Long-term mean sea level difference, Hilo-minus-Avila = 52 cm				

[1] 0/500 db average plus 49.0 dyn cm for 500/1,000 db average, based on TWZO data and 1,000 m stations.
[2] 0/500 db average plus 45.9 dyn cm for 500/1,000 db average, based on 37 stations in same 1-degree square.
[3] 0/400 db average plus 57.9 dyn cm for 400/1,000 db average, based on 25 stations in same 1-degree square.
* Correlation significant at 5% level.
** Correlation significant at 1% level.

the cause of the lower correlation for observations in 1-degree squares 93 and 95.

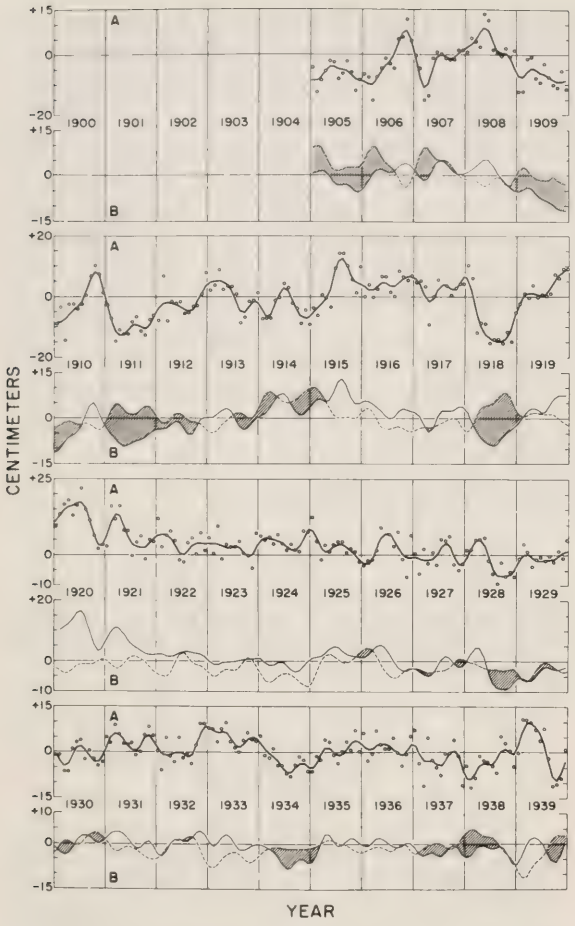
The correlations between monthly sea levels and offshore steric levels for the four stations in this study are less than anticipated from the results reported by other investigators, e.g., Shaw and Donn (1964) and Sturges (1966), as noted in the section, Earlier Studies. It is suspected that the lower correlations for the four Pacific stations in the present study may be due in part to comparison of a monthly sea level with a steric level from a single hydrographic observation on a given day. Present available steric data explain only about 40% of the variance of monthly sea levels from which the trend has been removed and which have been adjusted to normal pressure. As suggested by Stommel (1958) in relation to sea level at Bermuda, the possibility exists that geostrophically balanced barotropic currents exist which would also affect the monthly mean sea levels. When time series of frequent hydrographic observations or long-term observations from buoys become available to give a better estimate of continuous changes in steric level, we may then be able to attain a better understanding of the causes of sea level variations. For the present the unexplained variability may limit the use of sea levels and sea level differences to interpretation of broad-scale, highly anomalous oceanic changes.

NONSEASONAL SEA LEVEL DIFFERENCES

The monthly sea level differences used in this study are given in Appendix Tables 1 and 2 for Honolulu-minus-San Francisco and Hilo-minus-Avila, respectively. For each station the linear trends were removed and values adjusted to normal atmospheric pressure. The monthly differences reflect the adjustment, previously discussed, of the long-term mean sea level difference for all months and years to a mean difference determined from 0/1,000 db geopotential heights.

VARIABILITY

The nonseasonal variations are represented by the monthly anomalies, defined as the difference between the value for the month and the normal for the same month. The standard deviations in Table 1 for given months at individual stations exhibit the same characteristics as those reported in an earlier study (Saur, 1962) for six Pacific



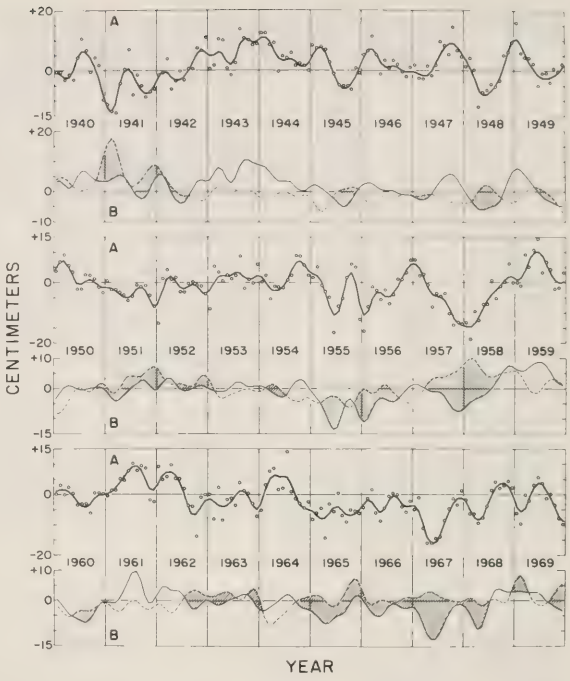


FIGURE 6.—Monthly sea levels (trend removed and adjusted to normal atmospheric pressure). Honolulu and San Francisco, 1905-69. A. Unsmoothed anomalies (circles) and smoothed anomalies (solid curve) for difference, Honolulu-minus-San Francisco. B. Smoothed anomalies for Honolulu (solid curve) and San Francisco (dashed curve). Shaded areas show periods when anomaly of difference is negative.

stations, two of which were Honolulu and San Francisco. Standard deviations in the former study were slightly larger because trends were not eliminated. At San Francisco, a coastal station at mid-latitude, the standard deviations show a seasonal change, attaining values near 6 cm in the late winter but decreasing to less than 3 cm in summer. At the other stations they vary less with season and those at the island stations generally lie in the range between 4.0 and 5.5 cm.

The standard deviations of the monthly sea level differences (Table 1) do not vary greatly throughout the year. The Honolulu-minus-San Francisco values are slightly larger than those for Hilo-minus-Avila because "climatic" changes, to be discussed later, appear in the longer Honolulu-San Francisco records.

The time series of the anomalies of monthly sea level difference are shown by open circles in Figure 6 for Honolulu-minus-San Francisco and in Figure 7 for Hilo-minus-Avila. The variability indicated by the standard deviations is evident. To suppress the shorter period variability and aid in detecting underlying longer period changes the time series have been smoothed, as indicated by the solid curves.

A simple 5-point smoothing operator with weights of $-1/16$, $1/4$, $5/8$, $1/4$, $-1/16$ was selected for the smoothing. This is a particular case of one-dimensional, two-element smoothers described by Shapiro (1970). It is a low-pass filter with a response function:

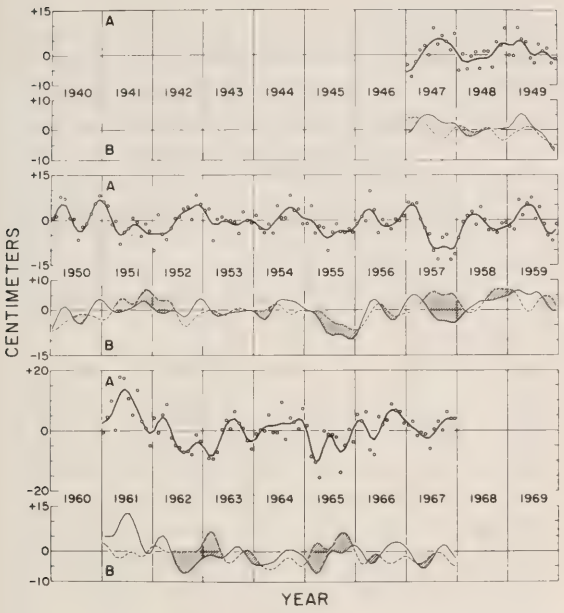


FIGURE 7.—Monthly sea levels (trend removed and adjusted to normal atmospheric pressure). Hilo and Avila, 1947-59 and 1961-67. A. Unsmoothed anomalies (circles) and smoothed anomalies (solid curve) for difference, Hilo-minus-Avila. B. Smoothed anomalies for Hilo (solid curve) and Avila (dashed curve). Shaded areas show periods when anomaly of difference is negative.

$$R(n) = 1 - \sin^4 \frac{\pi}{n}$$

where n is the number of data intervals in the Fourier component being smoothed. In our case n is also the wave period in months. Periods of 2 months are eliminated completely in one application of the smoother. Repeated applications of the smoother eliminate or reduce progressively longer periods. The response is a positive value between zero and one for all finite wave periods, so no 180° phase shift nor amplification occurs. The filter can be applied to the individual station anomalies followed by computation of the difference, or applied directly to the time series of the difference anomalies with the same end result.

The smoothed anomalies of monthly sea level for each station and of sea level differences in Figures 6 and 7 were obtained by applying the smoother eight successive times. The 50% level for the response function lies between periods of 5 and 6 months, and the response is 85% at 8 months.

CORRELATIONS BETWEEN HONOLULU-MINUS-SAN FRANCISCO AND HILO-MINUS-AVILA ANOMALIES

There are no independent data against which to check the anomalies of sea level differences as an index of nonseasonal variations in current. Since the two sets of differences span very nearly the same current region, the consistency between them is examined in this section to see if they agree reasonably well.

The correlations by month for both unsmoothed and smoothed anomalies are listed in Table 3. A general improvement of the correlations, particularly in winter, occurs as a result of smoothing to suppress the short-period variability. The effect of different scales of wind systems can be recognized by the seasonal pattern of correlations, especially in the smoothed anomalies. In the months from April through November when the subtropical high dominates the atmospheric pressure pattern over the North Pacific Ocean, all the correlations of smoothed anomalies are significant at the 1% level. In the months from November through March when meso-scale cyclonic and anticyclonic

TABLE 3.—Correlations of monthly sea level differences, by month Hilo-minus-Avila versus Honolulu-minus-San Francisco; $n = 20$ years.

Month	Unsmoothed anomalies	Smoothed anomalies
January	0.37	0.45*
February	0.37	0.44*
March	0.40	0.48*
April	0.56**	0.54**
May	0.45*	0.58**
June	0.63**	0.63**
July	0.64**	0.63**
August	0.41	0.69**
September	0.74**	0.68**
October	0.53**	0.56**
November	0.32	0.51*
December	0.57**	0.49*

* Correlation significant at 5% level ($r \geq 0.42$).
** Correlation significant at 1% level ($r \geq 0.54$).

wind systems move through the region, the correlations are somewhat lower, but still significant at the 5% level.

For the entire 20 years of concurrent records for Hilo-minus-Avila and Honolulu-minus-San Francisco, the correlation of unsmoothed anomalies is 0.49 and for smoothed anomalies it is 0.55. The 1% level of significance for the correlation coefficient of a sample of 240 months is 0.17, so these values are highly significant.

A visual comparison of the data in Figures 6 and 7 reveals the agreement evidenced by the correlation coefficients. Smoothed anomalies of the same sign tend to occur at the same time. For the most part the oscillations of the smoothed anomalies of sea level difference are in phase. Oscillations are noticeably out of phase in the periods October 1950-February 1951, March 1952-January 1953, September 1955-June 1956, and January-July 1958. In the last 18 months of the Hilo-minus-Avila record (July 1966-December 1967) the changes are similar to those for Honolulu-minus-San Francisco, but the smoothed anomaly of the difference is positive rather than strongly negative. Except for the 1955 periods, the nonagreement of the anomalies during these periods results mainly from a rise in sea level at San Francisco as opposed to a drop at Avila. These periods comprise only 20% of the total 20-year coincident records. In the remaining 80% the correlation coefficient for unsmoothed anomalies is 0.65 and for the smoothed anomalies it is 0.76. Both are significant well beyond the 1% level of 0.186 for a sample of 190.

CURRENT CHANGES INFERRED FROM SEA LEVEL DIFFERENCES

In this section some characteristics of the 65-year record of anomalies of sea level differences, Honolulu-minus-San Francisco are described with emphasis on their implications regarding changes in surface currents. Because the smoothed anomalies minimize local effects near the station, such as the set-up by wind and eddy systems passing near the Hawaiian Islands, they will be used as more realistic estimates of the larger scale and longer term changes in circulation. The term *current index* will be applied to this usage.

The discussion will follow the basic premise in this paper, that the currents are geostrophically related to the sea level difference so that a positive current index indicates above normal current, i.e., stronger flow to the south around the eastern limb of the anticyclonic gyre of the North Pacific Ocean. Conversely, negative current indexes indicate a below-average slope of the sea surface and proportionally weaker circulation.

Three tables have been compiled to show the characteristics of the current indexes. Table 4 gives statistical data regarding the current indexes by month. The data describe the year-to-year variations that occur. The normal monthly sea level differences, d, (of unsmoothed data) are repeated from Table 1 as a reference against which to measure the ranges and standard deviations of the current indexes.

Visual inspection of the time series (Figure 6) indicates that there are a number of different "climatic periods" in the record, i.e., periods characterized by the variability and the mean level of the current index during the period. Table 5 identifies seven such periods, into which I have subjectively divided the time series, and gives the mean and the standard deviation about that mean for each period. Obviously, other investigators might well select different climatic periods based upon other criteria related to their work.

In Table 6, highly anomalous periods have been identified on the basis of a criterion that the magnitude of the current index exceeded 10 cm for two or more consecutive months. As well as information on the dates, sign, magnitude, and duration of the current index, data are also given on the sign, magnitude, and date of the largest monthly sea level index at Honolulu and San Francisco which coincided with the current index greater than 10 cm.

Some observations which may be made about the Honolulu-minus-San Francisco differences and the information in these tables are given below.

1. The standard deviations of year-to-year changes for a given month (Table 4) vary from

TABLE 4.—Variability of current index (smoothed anomaly of sea level difference), Honolulu-minus-San Francisco, by months. $N = 65$ years. Standard deviation (s); largest positive and negative departures (Max and Min) and year of occurrence; Range (R) in centimeters and in percent of normal monthly sea level difference, $\bar{d}$ (from Table 1).

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
s (cm)	5.7	6.0	6.2	6.0	5.7	5.5	5.4	5.2	5.1	5.2	5.3	5.4
Max (cm)	11.2	13.5	15.3	16.0	16.5	17.4	17.7	15.8	11.4	10.3	9.5	10.6
Year	1920	1920	1920	1920	1920	1920	1920	1920	1920	1943	1943	1948
Min (cm)	−14.7	−14.4	−13.0	−14.0	−16.1	−15.4	−14.2	−14.6	−14.5	−13.5	−13.7	−14.4
Year	1958	1958	1958	1967	1967	1967	1918	1918	1918	1918	1957	1957
R (cm)	25.9	27.9	28.4	30.1	32.6	32.7	31.9	30.4	25.9	23.8	23.2	25.0
$R/\bar{d}$, (%)	52	54	49	50	53	54	53	49	43	39	40	47
$\bar{d}$ (cm)	50.6	51.9	57.4	60.3	61.7	60.6	59.6	61.1	60.8	60.7	57.8	53.5

5.1 cm in September to 6.2 cm in March. The seasonal change is due to greater winter-time variability at San Francisco (Saur, 1962) probably caused by year-to-year differences in weather conditions. A range of two standard deviations is nearly the same as the 11 cm range of the normal seasonal cycle. Long-term non-seasonal changes exceed ± 10% of the normal over one-third of the time.

2. The range between extremes (Table 4) in any given month varies from 23.2 cm for November to 33.7 cm in June. These are 39% and 54%, respectively, of the normal sea level differences for these months.

3. The minimum current index was —16.1 cm in May 1967 and the maximum was +17.7 cm in July 1920. The range between the extremes of the current index is 58% of the long-term mean sea level difference of 58 cm for Honolulu-minus-San Francisco, and it is three times as large as the range of the normal seasonal cycle.

4. The periods 1905-15, 1939-41, and 1955-69 were characterized by large changes between positive and negative values of current index over periods up to a few years, but on the average the indicated current is weaker than normal (Table 5).

5. During the periods 1915-25 and 1942-49, the current index implies moderate to large changes in current over periods of several years but indicates on the average a current stronger than normal. Except for large negative values in 1918, the current index indicates almost continuously stronger-than-normal circulation from mid-1915 through 1925.

6. The current changes during the periods 1926-38 and 1950-54 were relatively small as compared to the rest of the records. The current index did not exceed 8.5 cm and was nearly evenly distributed between negative and positive values.

7. The sea level records imply that unusually weak currents (negative anomalies in Table 6) occurred in 1911, 1918, 1941, 1957-58, and 1967, and that the periods of unusually strong currents occurred in 1915, 1920-21, 1943-44, 1948-49, and 1959.

8. During 7 of the 10 highly anomalous periods in Table 6, the absolute value of the monthly sea level anomaly at Honolulu is much larger than that at San Francisco. This indicates that significant changes in physical conditions which affect circulation occur in the central water of the current gyre as well as in the boundary current itself.

CONCLUDING REMARKS

For the investigation of historical changes in the ocean environment two notable observational deficiencies are apparent: the paucity of time-series subsurface data and the lack of information on changes in current of periods from a few months to several years. This study has attempted to develop some information on the normal seasonal cycle and the nonseasonal change of ocean currents in that part of the eastern

TABLE 5.—Mean current index, $\bar{\Delta}d$, and standard deviation, s, Honolulu-minus-San Francisco, for selected "climatic" periods (see text).

Years	Number of months	$\bar{\Delta}d$ (cm)	s (cm)
1905-14	120	−3.0	5.3
1915-25	132	3.5	6.1
1926-38	156	0.2	3.6
1939-41	36	−1.2	6.3
1942-49	96	2.6	4.8
1950-54	60	0.1	3.4
1955-69	180	−1.9	5.6

North Pacific Ocean which includes the California Current, using the most appropriate long-term records of sea level available.

Monthly sea level differences for a 65-year period (1905-69) between Honolulu and San Francisco and for 20 years (1947-59, 1961-67) between Hilo and Avila were computed to indicate the strength and fluctuations in the monthly geostrophic current around the eastern limb of the anticyclonic gyre of the North Pacific Ocean. The premise is that through the geostrophic relationship the nonseasonal variations of sea level difference indicate proportional changes in the current.

The distance between tide stations in each pair is about 3,900 km. The current structure is not uniform across the geographic region. Variability in the records is introduced by local conditions, and smoothing has been used to minimize these effects. Therefore, the sea level differences presented here can be indicative of only large-scale changes in circulation and conclusions regarding the circulation have been confined to periods of the more persistent highly anomalous periods in the sea level differences. In the tropical and western North Pacific where islands are more suitably located with respect to the currents the procedures followed here might be used to study variations in the Equatorial Currents and the Kuroshio.

In the Northeast Pacific there is no independent set of long-term observations to substantiate the inferences regarding current changes that have been drawn and no other islands for improving the network of tide stations. This lack emphasizes the desirability of frequent sections of subsurface observations between Cali-

TABLE 6.—Highly anomalous periods of sea level difference Honolulu-minus-San Francisco, 1905-69, identified by current index magnitude greater than 10 cm for at least two consecutive months.

Difference[1]													
1. Sign of anomaly	Negative	Positive	Negative	Positive	Negative	Positive	Positive	Negative	Positive	Negative	Positive	Negative	
2. No. of months, magnitude of anomaly >10 cm	4, (1)[2]	3	7	9, (3)	3	2, (2)	2	6	2	4			
3. Dates, magnitude of anomaly >10 cm	Mar.-June 1911 (Oct. 1911)	July-Sept. 1915	May-Nov. 1918	Jan.-Sept. 1920 (Feb.-Apr. 1921)	Jan.-Mar. 1941	Sept.-Oct. 1943 (Jan.-Feb. 1944)	Dec. 1948-Jan. 1949	Oct. 1957-Apr. 1958	May-June 1959	Apr. 1967-July 1967			
4. Largest anomaly, cm	−12.8	+12.9	−14.6	+17.7, (+13.7)	−13.6	+11.2 (+11.2)	+10.9	−14.7	+10.3	−16.1			
5. Total months duration, anomaly of same sign	22	23	11	80	23	32	8	18	19	45			
6. Inclusive dates for 5	Jan. 1911-Oct. 1912	May 1915-Mar. 1917	Mar. 1918-Jan. 1919	Feb. 1919-Oct. 1925[3]	Oct. 1940-Aug. 1942[4]	Sept. 1942-May 1945	Oct. 1948-May 1949	Apr. 1957-Sept. 1958	Oct. 1958-Apr. 1960[5]	Sept. 1964-June 1968			
Honolulu[1]													
7. Sign of anomaly	Negative	Positive	Negative	Positive	Positive	Positive	Positive	Negative	Positive	Negative			
8. Largest anomaly, cm, during 3 above	−9.4	+13.1	−9.2	+16.6 (+11.0)	+5.0	+10.6 (+8.5)	+7.8	−7.6	+9.2	−12.4			
9. Date of largest anomaly	May 1911	Aug. 1915	July 1918	July 1920, Mar. 1921	Mar. 1941	Sept. 1943, Jan. 1944	Jan. 1949	Nov. 1957	June 1959	May 1967			
San Francisco[1]													
10. Sign of anomaly	Positive	Positive	Positive	Negative	Positive	Negative	Negative	Positive	Negative	Positive			
11. Largest anomaly, cm, during 3 above	+4.6	+0.4	8.6	−4.2, (−2.7)	+17.7	0, −3.3	−3.8	+10.0	−1.6	+3.7			
12. Date of largest anomaly	Mar. 1911	Sept. 1915	Oct. 1918	Mar. 1920, Mar. 1921	Feb. 1941	Sept. 1943, Feb. 1944	Dec. 1948	Feb. 1958	May 1959	May 1967			

[1] All data refer to the smoothed anomalies depicted in Figure 6.
[2] ( ) secondary maximum or minimum in the same period.
[3] Ignores −0.4 cm in October 1923.
[4] Ignores +0.9 in June 1941.
[5] Ignores −0.3 cm in November 1959.

fornia and Hawaii. One would like information on the strength of the California Current, on the role of upwelling in the variations of the current, about the movement of the boundary or transition zone between the central water mass and the waters of the California Current, and about the interconnection between the California Current and the North Equatorial Current. The large changes in sea level at Honolulu as compared to San Francisco during periods of strong anomalies in the sea level difference (Table 6) raise the question as to how the California Current may vary in strength or width in relation to changes in the central water mass and position of the eastern North Pacific anticyclonic current gyre. Such environmental information has important applications for advisory services and forecasting for fisheries along the west coast of the United States.

One consequence of the preliminary work with sea level differences (Saur, 1966) mentioned earlier was the start of a pilot program of expendable bathythermograph observations between Honolulu and San Francisco aboard a merchant ship (Saur and Stewart, 1967) in June 1966, which continued at a frequency of up to 20 sections per year through 1970. Although the period of observation is very short as compared to the sea level records, it is hoped that the analysis of these observations can better define conditions related to the anomalous weak circulation in 1967 inferred from the sea level records, and shed light on the more specific problems mentioned above.

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It is a pleasure to submit this contribution honoring Dr. O. E. Sette, a great scientist, associate for many years, and friend. This exploratory investigation of sea level differences is one outgrowth of many stimulating discussions with him on environmental variability and its implications to fisheries.

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APPENDIX TABLE 1.—Honolulu-minus-San Francisco, 1905-69. Monthly sea level difference (linear trend removed and adjusted to normal atmospheric pressure at each station) in centimeters. The long-term mean difference for all months and years has been adjusted to 58 cm, as explained in text, by reference to 0/1,000 db geopotential heights.

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1905	46.7	39.5	48.6	54.7	59.6	58.2	51.5	54.8	58.6	54.9	45.9	45.2
1906	43.8	44.1	42.1	52.9	(57.3)[1]	59.2	56.6	56.3	65.9	66.6	69.4	58.1
1907	50.2	47.1	42.3	46.8	60.5	61.5	59.6	59.6	58.9	59.0	59.4	55.1
1908	51.5	57.6	61.5	62.8	75.1	72.0	61.1	61.5	60.2	62.8	56.9	54.8
1909	38.4	39.9	56.0	59.6	53.7	51.3	56.6	54.2	50.7	49.7	52.4	41.9
1910	41.8	48.8	43.0	58.0	59.4	56.6	57.3	61.8	67.2	71.4	65.4	54.7
1911	48.0	44.7	42.6	49.7	49.2	48.5	51.7	54.7	49.3	48.0	50.4	47.6
1912	42.8	58.9	49.3	59.0	59.4	59.1	54.0	55.9	57.7	57.9	58.9	61.6
1913	52.8	55.9	66.5	62.7	65.4	64.1	60.6	52.4	54.0	59.4	56.8	55.0
1914	43.3	45.0	50.5	59.3	61.6	65.3	62.7	58.9	56.9	51.9	53.7	44.4
1915	47.2	45.7	58.2	59.9	58.2	69.2	74.2	75.5	70.4	66.5	59.2	63.6
1916	50.7	56.2	57.1	63.0	68.6	67.5	61.2	61.0	69.4	67.3	63.2	60.7
1917	55.3	57.5	60.7	51.2	62.0	66.5	64.3	64.8	61.3	63.7	62.3	57.7
1918	61.3	58.2	45.5	51.9	52.7	45.3	45.8	47.2	45.3	49.4	43.0	48.0
1919	48.5	53.2	56.9	64.3	61.4	61.6	59.8	62.2	68.4	66.8	67.3	62.8
1920	60.4	65.5	73.9	78.4	74.5	76.6	81.6	76.1	72.1	67.5	59.8	56.9
1921	53.4	68.0	68.7	76.6	69.6	68.6	59.1	65.2	67.0	59.1	62.9	57.6
1922	62.6	54.4	63.8	68.3	66.3	58.7	57.1	65.0	66.4	60.8	65.1	54.7
1923	56.3	52.3	66.9	58.8	65.1	63.2	62.2	65.6	61.0	60.8	53.3	60.5
1924	56.7	56.6	63.2	63.7	68.4	64.3	60.9	64.6	62.1	61.6	65.8	60.8
1925	63.0	56.3	55.5	63.7	62.5	64.1	64.0	65.3	61.3	62.8	58.7	51.1
1926	46.9	50.0	55.7	61.9	70.6	67.7	66.3	63.7	68.3	59.1	50.4	59.8
1927	51.0	45.4	59.3	57.3	62.5	57.1	64.7	65.5	66.9	57.5	52.6	50.5
1928	52.2	53.7	62.3	65.6	67.4	58.8	53.2	51.4	58.1	53.4	52.2	46.1
1929	49.3	55.6	58.2	56.2	60.2	59.9	57.4	60.7	58.1	62.0	56.5	58.4
1930	49.5	51.1	50.7	53.8	62.7	63.9	63.7	58.4	61.3	58.3	53.1	50.2
1931	55.7	54.8	66.2	66.5	64.3	63.0	62.8	59.8	61.0	66.5	66.4	58.9
1932	50.9	45.9	62.3	58.9	58.3	65.5	57.6	60.8	56.8	63.1	67.4	62.7
1933	58.5	59.6	60.7	68.1	71.6	64.1	61.2	61.0	64.6	67.4	62.0	57.0
1934	56.1	50.8	55.3	61.7	57.2	56.4	52.6	53.0	56.7	59.4	55.2	47.3
1935	44.2	50.8	54.7	64.6	65.0	60.1	56.0	61.6	64.4	61.4	65.3	53.7
1936	57.2	49.0	57.0	67.7	64.2	61.8	61.0	66.0	60.3	56.2	57.3	59.0
1937	58.3	48.3	46.3	65.4	59.2	55.6	52.0	60.9	60.4	65.0	56.6	42.6
1938	46.5	40.3	49.1	59.4	58.9	57.4	55.1	54.2	66.3	63.6	58.4	48.8
1939	50.7	63.1	68.0	70.3	69.2	64.5	67.7	59.1	49.7	50.5	49.5	54.6
1940	50.0	51.3	53.9	58.9	58.4	65.0	70.3	67.8	60.0	65.1	59.6	43.6
1941	39.1	38.2	43.1	56.0	62.1	67.6	51.5	59.5	55.6	51.8	50.6	47.3
1942	49.0	51.2	61.2	54.0	58.1	60.2	56.3	61.6	61.2	68.2	64.3	64.4
1943	51.1	53.7	67.7	70.2	62.3	58.9	62.2	74.7	71.4	70.4	66.1	62.3
1944	63.0	64.3	65.6	69.5	61.2	65.4	63.6	67.0	62.3	63.2	59.1	53.2
1945	59.0	59.2	65.3	67.1	64.4	58.5	54.7	55.8	55.6	54.2	58.7	52.4
1946	55.6	58.5	68.7	65.4	60.3	64.1	60.3	64.3	62.6	60.0	55.5	54.5
1947	52.5	49.2	54.4	61.9	59.8	62.5	69.3	69.3	65.9	75.3	64.4	57.9
1948	51.9	56.2	57.5	48.3	54.4	54.2	55.1	55.6	57.4	65.9	64.1	63.0
1949	66.7	57.7	61.6	64.4	63.8	55.5	58.8	60.3	56.5	61.6	57.5	55.7
1950	54.5	58.9	66.5	65.9	65.0	58.3	57.3	63.6	63.0	61.8	56.0	49.9
1951	51.3	49.4	54.8	57.0	57.3	54.5	55.0	60.2	59.1	59.7	53.7	45.2
1952	37.0	53.3	61.5	61.3	63.4	57.4	56.3	60.7	61.0	59.6	56.5	49.5
1953	41.8	57.3	60.6	60.7	64.2	61.7	62.0	69.8	58.6	61.8	57.4	59.5
1954	50.6	54.4	51.6	59.1	59.9	58.7	60.4	63.5	69.7	69.4	63.0	55.7
1955	52.1	57.2	56.5	57.1	56.6	44.0	51.6	55.8	62.2	66.9	62.9	41.3
1956	34.5	43.9	55.9	57.7	55.8	58.2	52.5	57.1	62.0	61.7	61.2	61.0
1957	58.2	54.1	60.2	59.5	53.6	57.1	54.9	57.5	50.3	46.6	44.8	39.7
1958	37.6	33.3	47.9	47.8	54.6	53.5	60.5	55.7	59.6	61.2	64.2	53.4
1959	50.8	50.7	66.7	65.4	72.5	75.2	62.9	68.1	65.0	58.6	56.2	56.7
1960	50.3	55.2	57.0	62.9	62.0	56.9	55.8	58.0	54.4	61.3	58.3	53.5
1961	49.9	53.3	58.8	65.6	66.2	68.4	69.9	68.7	70.3	69.3	55.8	50.8
1962	59.9	56.7	63.2	70.2	66.6	65.8	61.4	57.2	56.7	46.9	56.9	53.5
1963	50.8	43.7	59.7	51.8	59.9	59.4	55.9	65.1	61.8	61.0	54.7	46.2
1964	45.5	55.1	65.1	69.0	63.2	62.7	73.8	61.9	59.2	(57.6)[1]	53.2	51.1
1965	42.3	45.9	52.9	45.9	58.6	54.7	60.2	54.0	51.5	55.7	52.2	47.0
1966	46.4	50.6	59.0	54.0	52.8	56.3	59.1	61.5	60.6	56.6	51.8	51.3
1967	45.5	51.0	46.1	44.2	45.6	46.2	45.8	52.5	56.0	59.3	54.1	54.9
1968	48.7	45.4	50.9	50.7	53.9	56.8	61.1	65.3	62.6	63.7	62.3	55.6
1969	44.3	42.1	57.3	58.0	64.8	66.4	63.3	59.5	60.9	57.2	49.8	43.5
N	65	65	65	65	64	65	65	65	65	64	65	65
MEAN	50.6	51.9	57.4	60.3	61.7	60.6	59.6	61.1	60.8	60.7	57.8	53.5

[1]Missing value was estimated by interpolation of anomalies.

APPENDIX TABLE 2.—Hilo-minus-Avila, 1947-59 and 1961-67. Monthly sea level difference (linear trend removed and adjusted to normal atmospheric pressure at each station) in centimeters. The long-term mean difference for all months and years has been adjusted to 52 cm, as explained in text, by reference to 0/1,000 db geopotential heights.

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1947	42.4	40.0	50.9	58.1	58.8	53.7	62.2	57.3	59.5	57.1	52.0	54.1
1948	40.8	47.9	48.5	56.0	56.7	49.2	54.4	54.9	48.7	57.2	53.6	55.9
1949	45.9	47.1	62.5	61.8	59.9	52.8	50.4	57.6	54.2	55.2	47.7	45.7
1950	46.5	48.6	60.9	63.2	55.8	54.1	46.3	51.6	51.7	54.8	56.1	55.1
1951	52.0	52.1	51.5	56.1	47.4	49.8	50.3	54.5	52.0	47.0	49.1	43.1
1952	35.7	49.2	48.3	49.7	52.6	54.3	54.2	57.5	57.4	52.7	58.8	52.1
1953	49.0	51.2	46.3	56.8	56.6	53.5	52.8	52.8	48.3	55.5	50.1	45.7
1954	47.5	44.7	48.7	55.1	51.0	58.6	53.8	54.4	61.2	55.7	54.2	45.4
1955	44.8	52.3	48.7	54.4	52.9	43.6	48.7	52.6	49.0	48.4	47.7	42.6
1956	45.0	48.8	52.7	66.2	58.9	49.4	53.4	52.3	49.8	53.1	50.0	48.3
1957	52.0	52.7	59.1	56.5	52.6	49.2	42.9	40.7	47.2	48.0	37.2	35.7
1958	40.7	47.0	54.9	59.5	53.9	58.4	53.2	50.4	49.7	48.4	49.5	46.1
1959	43.6	44.3	60.2	58.0	61.3	61.5	53.5	58.3	52.0	47.5	43.6	45.7
1960	--	--	--	--	--	--	--	--	--	--	--	--
1961	45.5	52.1	63.3	56.6	73.6	71.3	63.9	59.0	66.6	56.0	51.4	41.8
1962	50.4	46.6	58.7	65.4	53.0	48.9	47.4	46.6	46.3	44.8	49.2	43.3
1963	(39.5)[1]	38.3	43.8	49.4	55.9	57.5	53.8	60.3	55.5	53.6	47.0	40.7
1964	45.0	47.8	53.1	61.9	54.9	53.1	62.8	51.0	57.3	55.8	51.1	54.3
1965	47.9	38.8	42.8	40.9	55.7	52.6	52.0	51.7	39.1	48.0	51.1	43.1
1966	51.6	50.7	59.8	50.1	47.5	58.6	55.1	57.4	62.0	59.5	56.9	49.4
1967	47.8	50.8	51.5	56.1	54.4	47.9	53.9	57.1	53.0	59.3	54.5	51.2
N	19	20	20	20	20	20	20	20	20	20	20	20
MEAN	46.0	47.6	53.3	56.6	55.7	53.9	53.3	53.9	53.0	52.9	50.5	47.0

[1]Missing value was estimated by interpolation of anomalies.

TEMPERATURE TRENDS AND THE DISTRIBUTION OF GROUNDFISH IN CONTINENTAL SHELF WATERS, NOVA SCOTIA TO LONG ISLAND

JOHN B. COLTON, JR.[1]

ABSTRACT

The 1953 to 1967 downward trend in seawater temperature in continental shelf waters between Nova Scotia and Long Island did not significantly alter the distribution of four species of groundfish. There was an extension of the southern range of American plaice and a contraction of the northern range of butterfish. These shifts in distribution were not extensive. The equatorward boundary of American plaice appears to be limited by summer temperatures too high for survival and the poleward boundary of butterfish by summer temperatures too low for reproduction. There was no obvious alteration in the geographic distribution of haddock and yellowtail flounder. The distribution and movements of haddock and yellowtail flounder appear to be influenced more by restrictive spawning area and bottom type conditions than by temperature.

An alternation in sea-surface temperature has been observed at Atlantic coast stations from Nova Scotia to Cape Hatteras (Lauzier, 1965; Stearns, 1965; Welch, 1967). Coastal warming and cooling trends have been pronounced in the waters between Cape Sable and Long Island. A warming trend began in the early 1940's and reached a maximum during 1952-53. This rise in temperature was followed by a cooling period which continued with only minor checks through 1967. Since 1967 there has been an increase in sea-surface temperature, the 1969 annual mean being only slightly lower than the long-term mean. An example of these temperature trends is shown in Figure 1 in which the annual deviations from the 1940-1959 mean sea-surface temperature at Boothbay Harbor, Maine are plotted for the period 1940-1968. The base period 1940-1959 was chosen for it included approximately equal numbers of years in periods of warming and cooling.

In Figure 2 seasonal sea-surface-temperature curves at Boothbay Harbor based on monthly mean values for each year between 1940 and 1968 are compared with the 1940-1959 mean seasonal temperature curve. As would be expected, there were marked fluctuations in the seasonal temperature cycle due to variations in runoff and meteorological conditions, but for the most part, the monthly deviations reflected the annual deviations in both periods of warming and cooling.

Similar warming and cooling trends have occurred offshore, both at the surface and at depth (Taylor, Bigelow, and Graham, 1957; Lauzier, 1965, 1967; Colton, 1968a, 1968b, 1969). Though offshore temperatures varied less seasonally than those inshore, in general, the magnitude of both surface and subsurface temperature anomalies were greater offshore than along the coast. These warming and cooling trends are associated with changes in the composition of the subsurface water (Colton, 1968b, 1969). Cold years occur when slope water is displaced or modified by coastal water of Labrador origin. Warm years occur when slope water borders upon the 200-m isobath and the ratio of coastal to central Atlantic water is low.

Taylor et al. (1957) concluded that although there was evidence of northward shifts in the abundance and distribution of some marine animals as a consequence of the warming trend which commenced in the early 1940's, these

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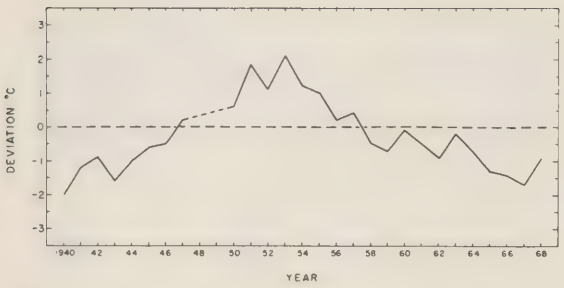

FIGURE 1.—Annual deviations from the 1940-1959 mean sea-surface temperature at Boothbay Harbor, Maine.

changes did not appear to have produced any obvious alteration of the general faunal characteristics of the Gulf of Maine. During the recent cooling period, there were a number of reports of southward extensions of range and shifts in the distribution of fish and invertebrate fauna: (1) Boyar (1964) reported the occurrence of the Greenland halibut (*Reinhardtius hippoglossoides*) off Boothbay Harbor, Maine, in February 1963. This is a southern shoal-water record for this subarctic species. (2) Substantial numbers of capelin (*Mallotus villosus*) were caught in the Bay of Fundy in the spring of 1965 (Tibbo and Humphreys, 1966) and have continued to be taken each spring through 1968 (S. N. Tibbo, personal communication). There has been no written record of the occurrence of capelin in this area since 1919 (Bigelow and Schroeder, 1953). (3) Since 1961, spiny dogfish (*Squalus acanthias*) have been collected with increasing frequency during the winter months in South Carolina coastal waters (Bearden, 1965). This species is uncommon south of Cape Lookout, N.C., and there have been no previous records of its occurrence off South Carolina. (4) Collette and MacPhee (1969) reported the collection of an arctic shanny (*Stichaeus punctatus*) in Massachusetts Bay in August 1968. This is the second record of this northern species in the Gulf of Maine and extends the known range 180 miles to the southwest. (5) Finally, the green crab (*Carcinus maenas*), which became abundant as far northeast as Nova Scotia in the mid-1950's, has declined in abundance, coincident with the decline in temperature. The green crab is now rare in Canada and eastern Maine, but still abundant in southwestern Maine and northern Massachusetts (Welch, 1968).

Such observations of northward and southward shifts in the abundance and distribution of marine animals have usually been based on sporadic observations and on commercial fishery statistics. The accumulation of records of occasional occurrences over a number of years can give the impression of a change in distribution sustained over a period of time. Many of the fluctuations in commercial fishery landings are due to changes in fishing methods, efficiency, effort, and market conditions. As Bell and Pruter (1958) have demonstrated, it is deceptively easy to infer relationships and draw false conclusions from such data. Given adequate research vessel surveys, however, it should be possible to determine the relative abundance and distribution of fish and invertebrate fauna with some precision. In this paper such otter-trawl survey data are used to determine what effect the recent cooling trend has had on the distribution of some of the important commercial species of groundfish in continental shelf waters between Nova Scotia and Long Island.

A great diversity of pelagic, hemipelagic, and demersal fish species were caught during the otter-trawl surveys. Our initial analysis was limited to the relatively abundant commercially exploited groundfish species felt to be representatively sampled by the otter trawl, e.g., those species living on or in close association with the bottom and within the depth limits covered by the surveys (approximately 30-350 m). For this study, four species were selected which represent the basic types of geographic zonation characteristic of the area. The general geographic distribution of these species is as follows:

AMERICAN PLAICE (*HIPPOGLOSSOIDES PLATESSOIDES*)

The plaice is an arctic-boreal species which is found in abundance from Greenland to Cape Cod. In the Gulf of Maine this species is most plentiful in depths ranging from 30 to 200 m.

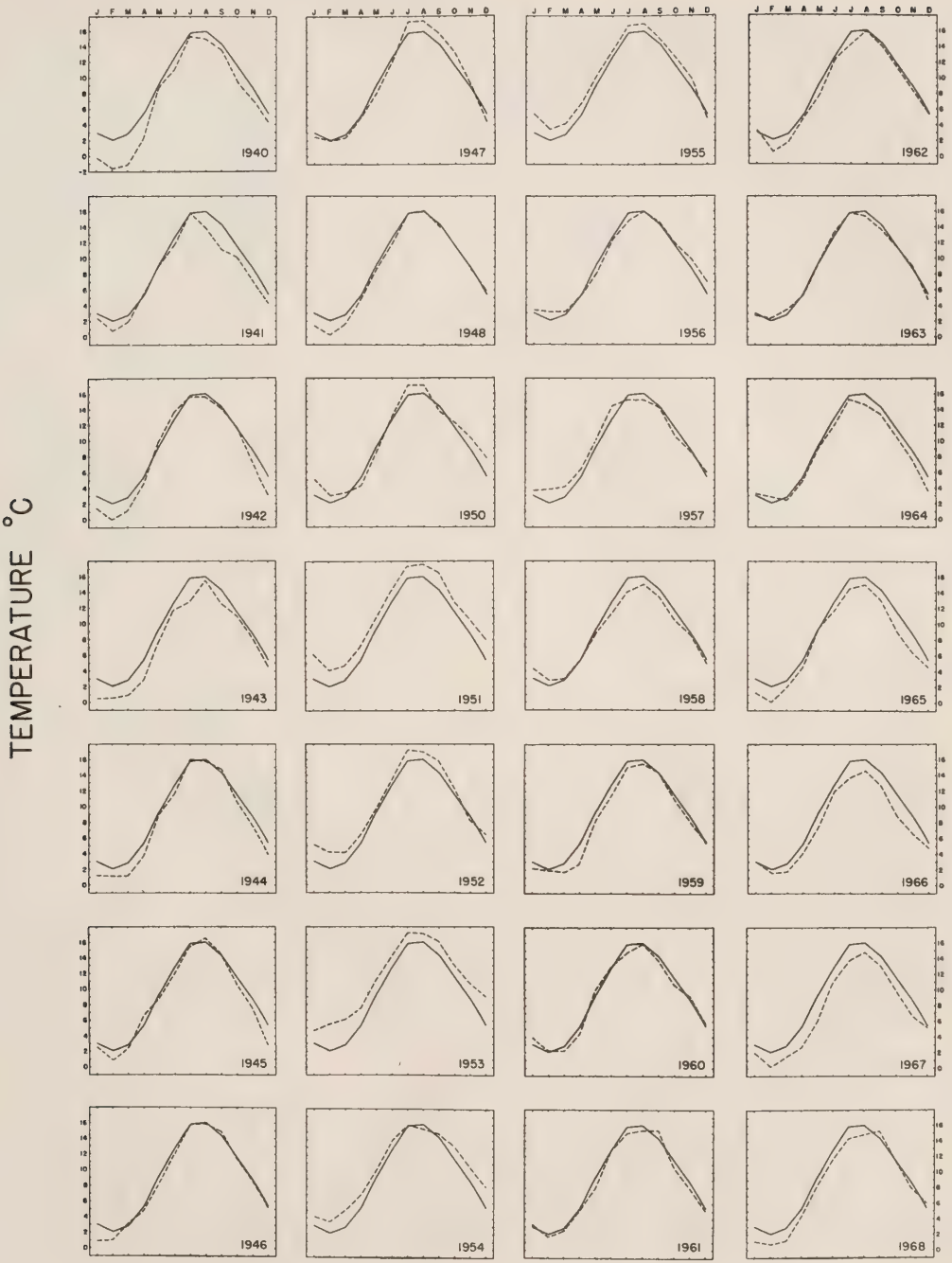

FIGURE 2.—1940-1959 mean and yearly seasonal temperature curves, Boothbay Harbor, Maine. Solid line: 1940-1959 mean, dashed line: individual year. The 1949 records are incomplete and have not been included.

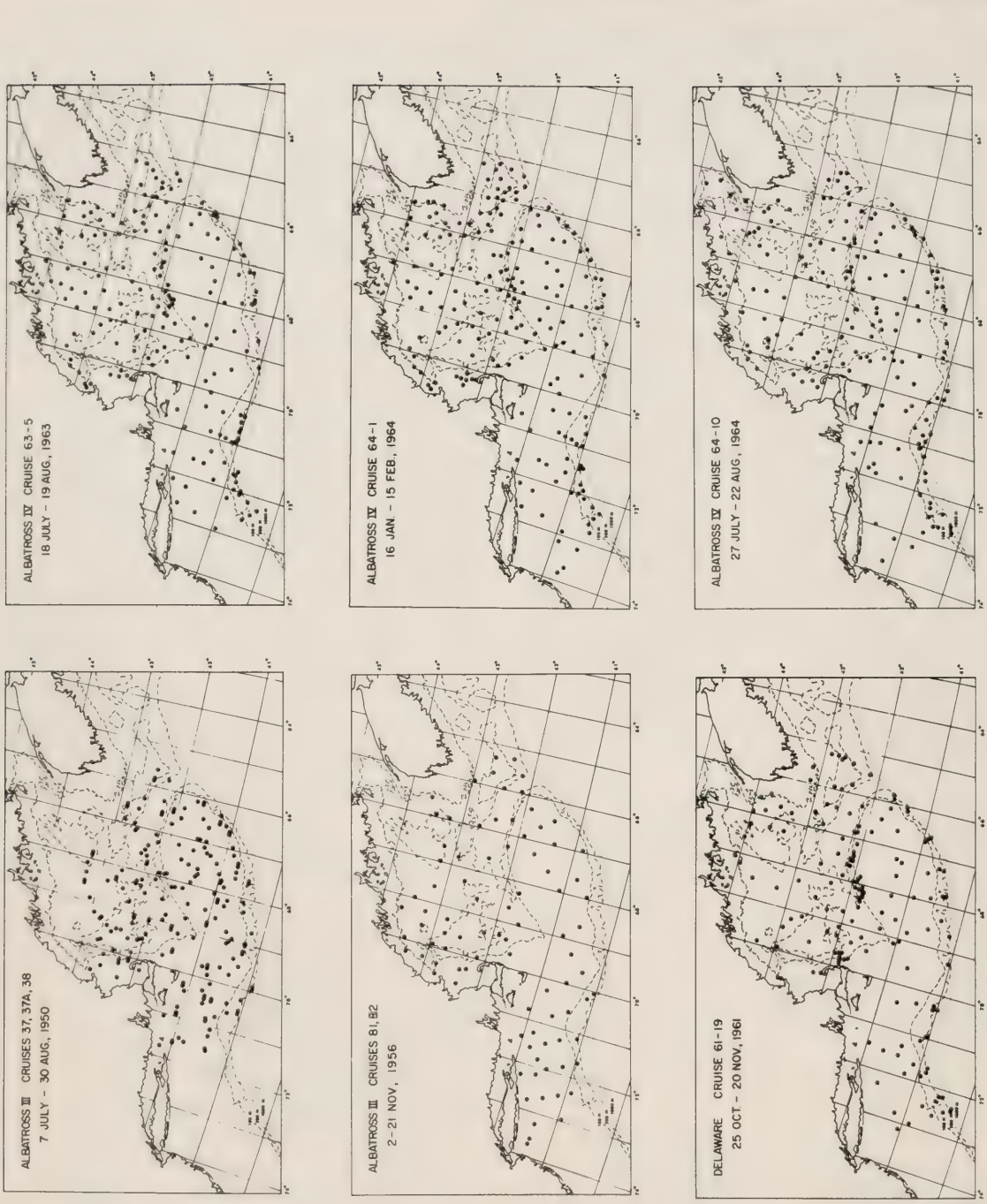

FIGURE 3.—Dates and station locations of groundfish cruises, July-August 1950 through July-August 1964.

Cape Cod (lat 40°30'N, long 70°00'W) marks the southern and western limits of its normal range, although plaice are occasionally taken west to Block Island. Tagging experiments in the Grand Banks area (Pitt, 1969) suggest that there are a number of relatively sedentary populations of plaice and that the limited migrations that do occur are associated with spawning and feeding patterns. Research ship and commercial catch statistics indicate that this is also true of the Gulf of Maine populations.

HADDOCK (*MELANOGRAMMUS AEGLEFINUS*)

The haddock is a boreal species inhabiting both sides of the North Atlantic whose distribution, for the most part, is confined to waters shoaler than 200 m. On the American coast the westerly limit of its normal occurrence is the Nantucket Shoals area (long 70°00'W) although in winter haddock are sometimes taken in the area between Nantucket Shoals and New Jersey. Young-of-the-year haddock are found in the area between Nantucket Shoals and Hudson Canyon during the summer and fall. Indications are that the majority of these young fish are concentrated at mid-depths (Colton, 1965) and caught while the trawl is being set out and retrieved. Young-of-the-year haddock are not included in the catch statistics presented in this paper. Tag returns and the distribution of commercial fishing effort indicate that in comparison with the cod, the haddock is a relatively stationary fish, and except for short-term shifts in depth distribution they do not follow any regular migratory routes (Needler, 1930; Schroeder, 1942; Schuck, 1952).

YELLOWTAIL FLOUNDER (*LIMANDA FERRUGINEA*)

The yellowtail flounder is a shallowwater species which occurs along the Atlantic coast of North America from Labrador to New Jersey. The bulk of the catch is taken in water shoaler than 100 m. The yellowtail flounder is one of the few species which is common both to the east and west of Cape Cod at all seasons of the year. The tagging studies of Royce, Buller, and Premetz (1955) and Lux (1963) show that, in general, the populations of New England yellowtail are to be found in relatively localized groups which may make short seasonal migrations and only a limited amount of mixing takes place between groups.

BUTTERFISH (*PEPRILUS TRIACANTHUS*)

The butterfish ranges in the northwestern Atlantic from the outer coast of Nova Scotia and Cape Breton to northern Florida. There is a separate population in the Gulf of Mexico (Caldwell, 1961). This temperate-region species is only a warm season migrant to coastal waters off New England and the Maritime Provinces. In general, butterfish appear off southern New England at the end of April, but it is not until July that they are plentiful in the inner parts of the Gulf of Maine and on Georges Bank. Butterfish disappear from the coast by the end of December at the latest.

COLLECTION AND REDUCTION OF DATA

The data were collected during the period 1950-1968 by personnel at the Bureau of Commercial Fisheries (now the National Marine Fisheries Service) Biological Laboratory, Woods Hole, Mass., on surveys designed to determine the distribution and relative abundance of groundfish in the Gulf of Maine and adjacent waters. The fishing gear used during these surveys was similar to that being used by the commercial haddock fleet at the time. A 1½ Iceland trawl was used prior to 1951, and a No. 36 redfish trawl has been used since that time. A description of these trawl nets is given by Knake (1956). The cod end and top belly of both type nets were lined with fine mesh netting to retain smaller fish. Three vessels were used in these surveys; the side trawlers *Albatross III* and *Delaware* and the stern trawler *Albatross IV*. On all cruises the trawl was towed for 30 min at each station at a vessel speed of approximately 3.5 knots. Various sampling patterns employing both random and grid station

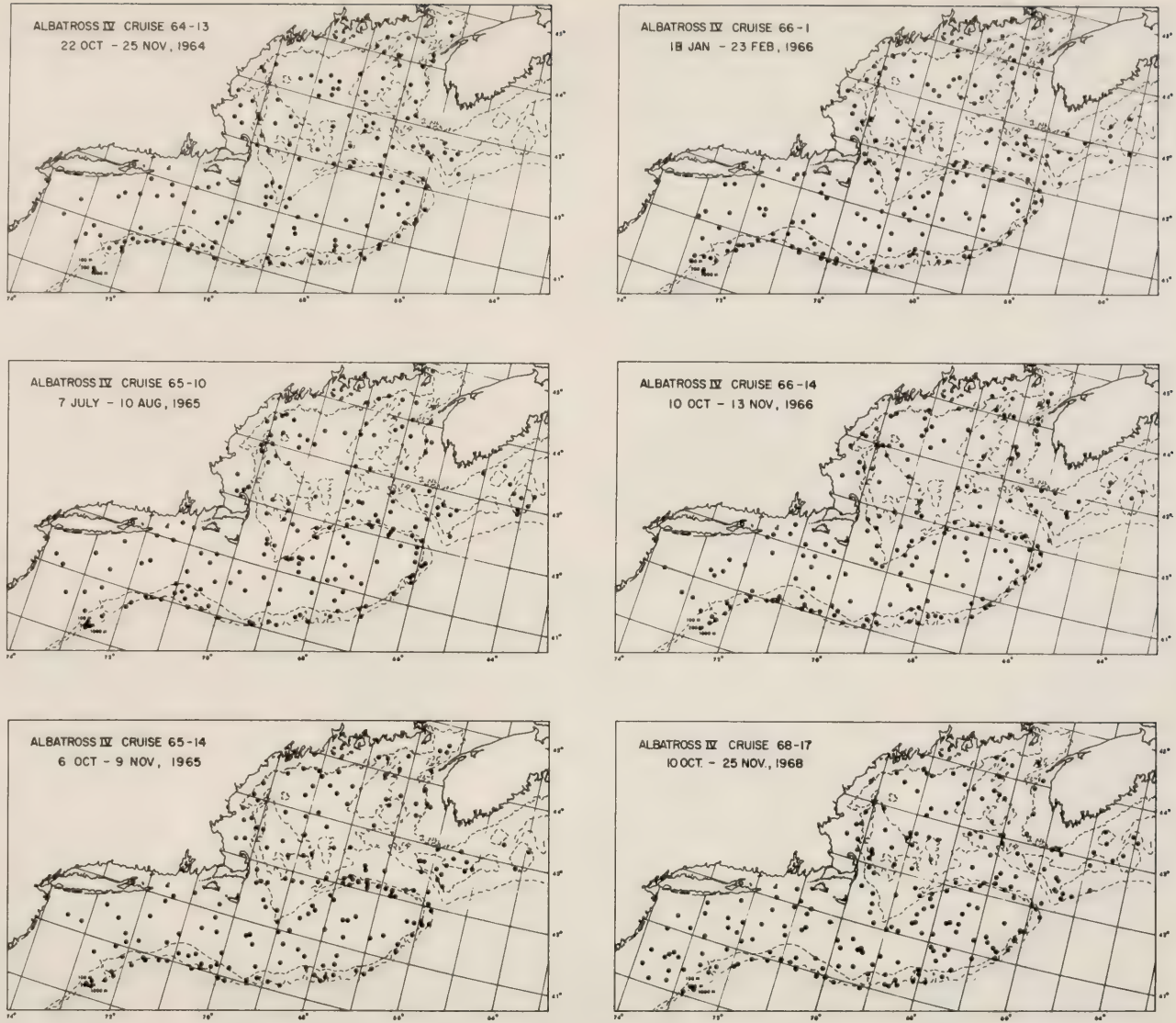

FIGURE 4.—Dates and station locations of groundfish cruises, October-November 1964 through October-November 1968.

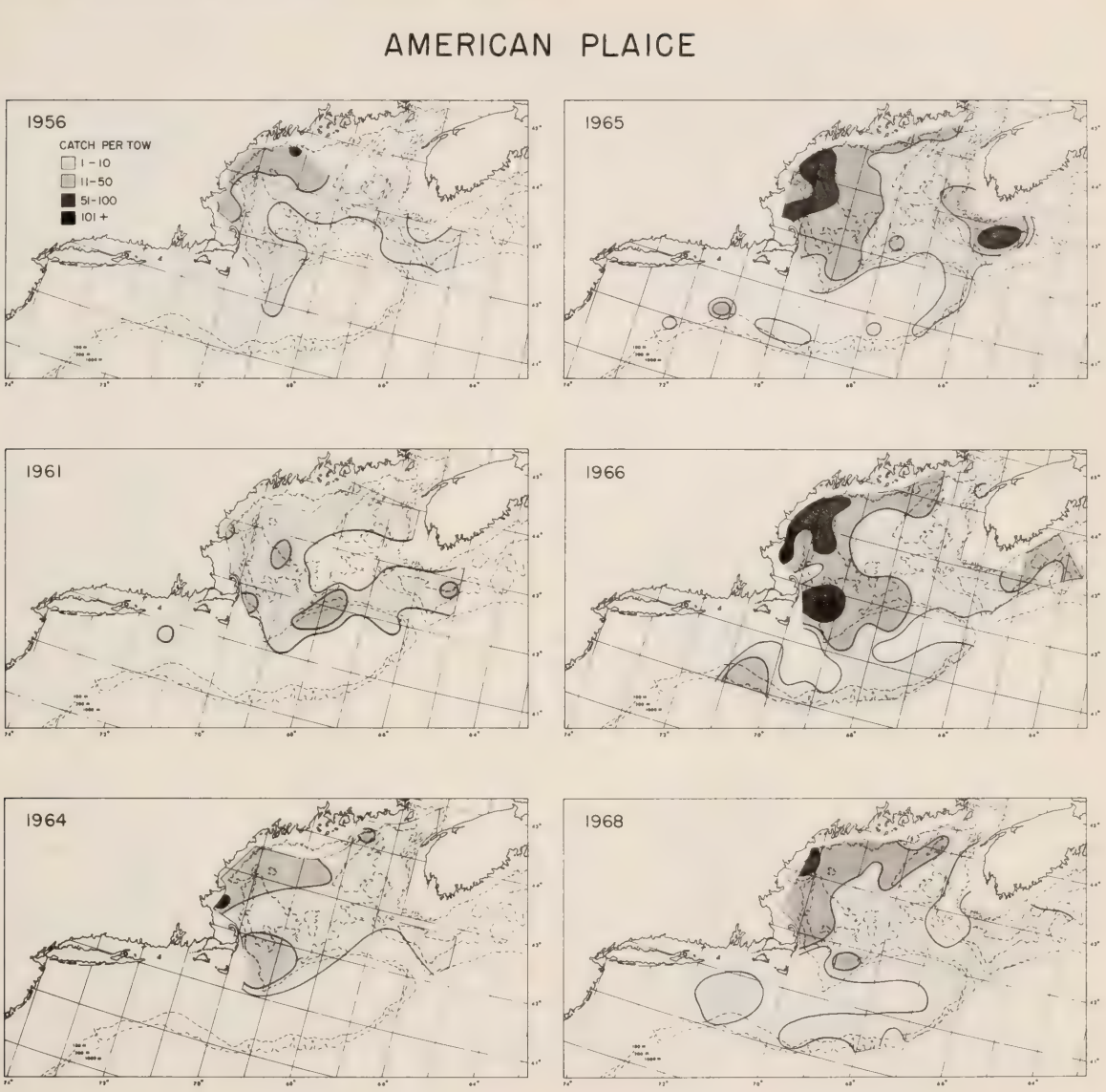

FIGURE 5.—Distribution of American plaice during October-November.

designs were used, but for most cruises a stratified random sampling technique was employed in which station location and number were prorated by area and depth zone. A complete description of the sampling design currently being employed is given by Grosslein (1969).

Although an effort was made to standardize sampling techniques, comparative tows made with the *Albatross III* and the *Delaware* and the *Albatross IV* and the *Delaware* showed that fishing efficiency varied to some extent between vessels and with towing methods (stern vs. side trawling). Fishing efficiency also varies with time of day and with species and age of fish (Bigelow and Schroeder, 1953; Colton, 1965; Fritz, 1965). However, for the purpose of de-

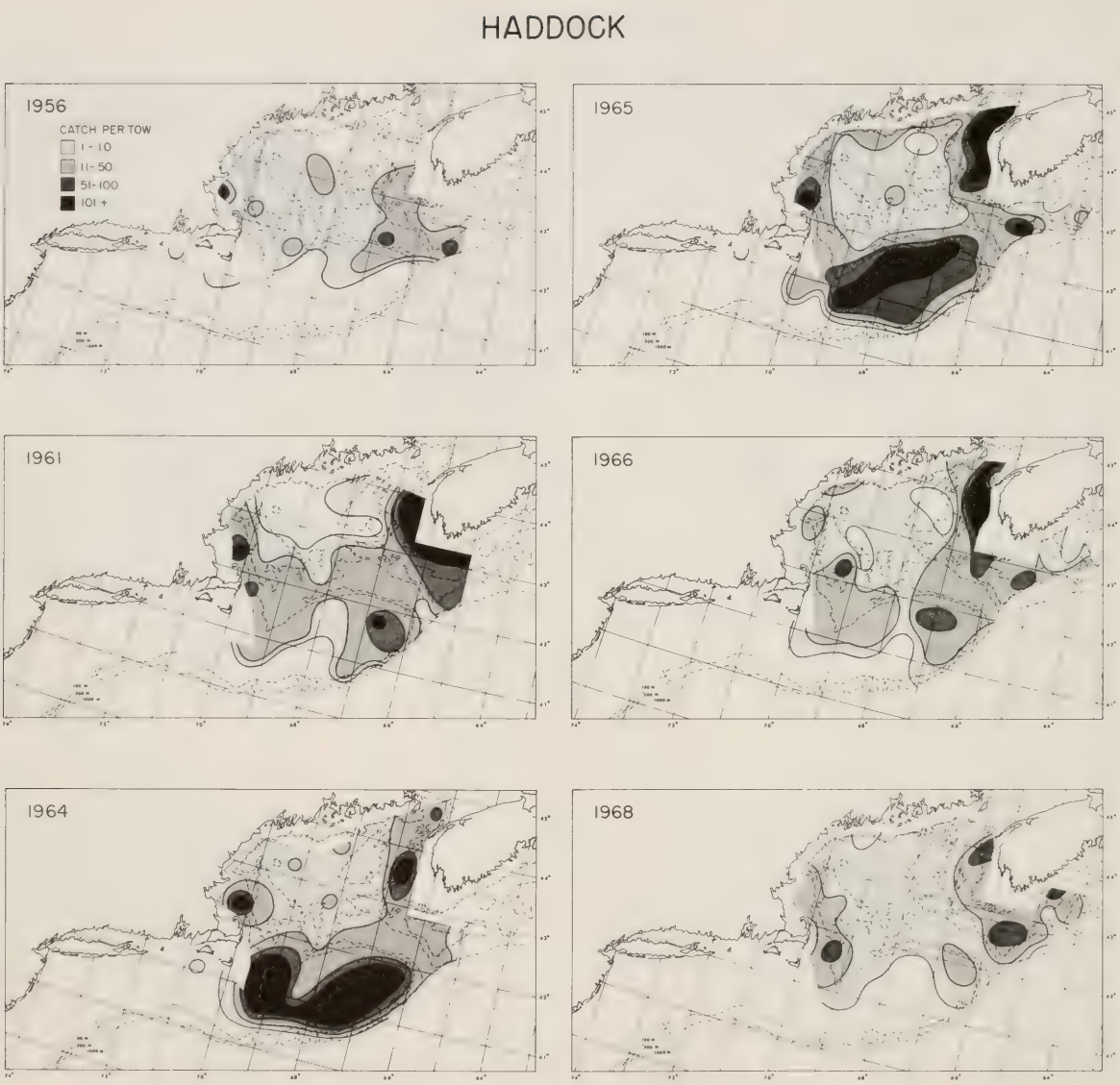

FIGURE 6.—Distribution of haddock during October-November.

lineating the general distribution patterns of the species of fish considered in this paper, the survey data would appear to be adequate.

For most species and in most areas there were marked differences in the catch at adjacent stations. In preparing the species distribution charts, the average number of fish per tow for all stations lying within 30″ latitude and longitude quadrangle areas was determined. The contour lines were drawn on a basis of these average values entered at the center of each 30″ quadrangle. Considerable smoothing and interpolation were still necessary, especially in cases where the bathymetry required adjustments in order to avoid contouring a species outside its normal depth range as indicated by individual

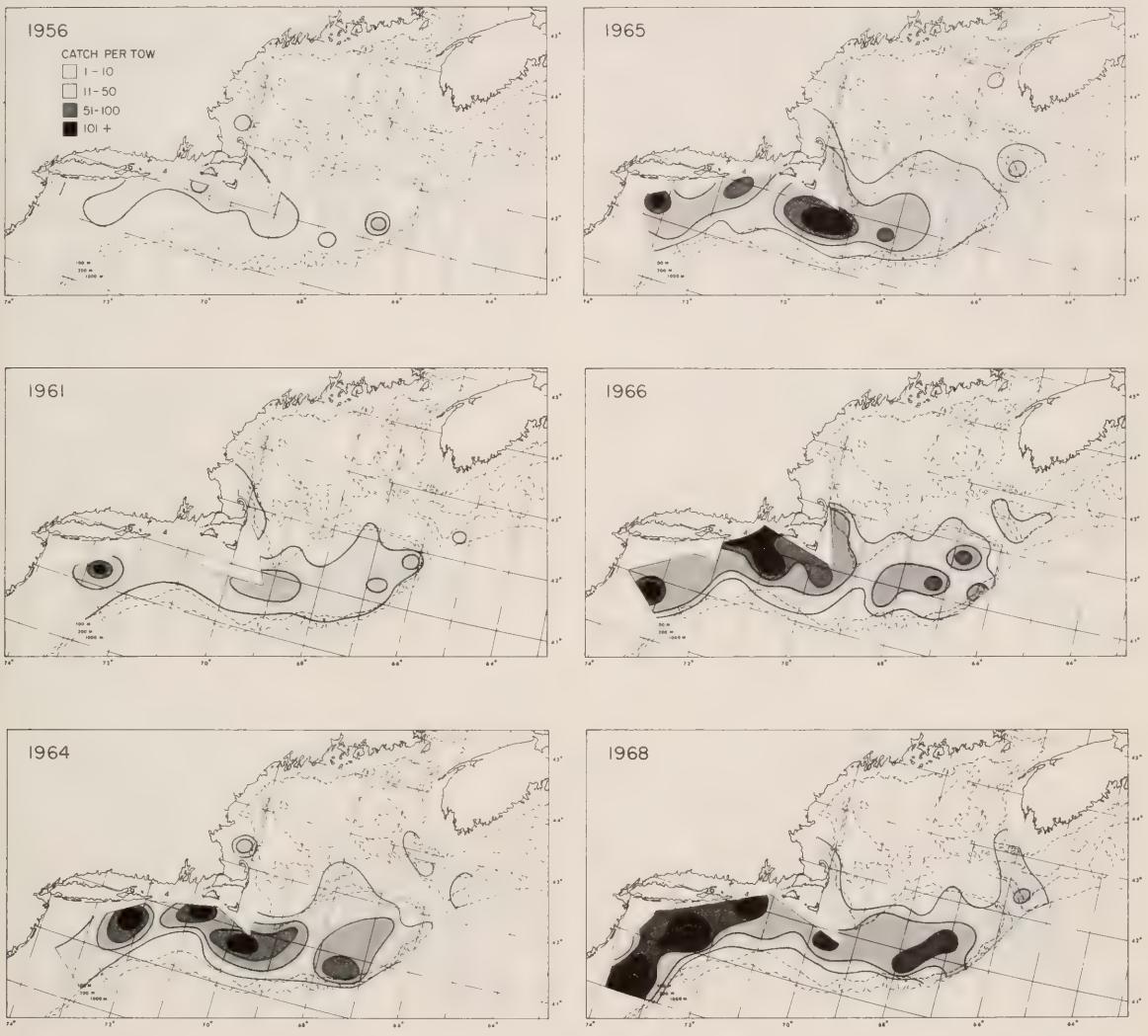

FIGURE 7.—Distribution of yellowtail flounder during October-November.

station data.

Groundfish surveys were conducted principally during the fall months in an effort to estimate the strength of new year classes of haddock, but some surveys were made at other seasons of the year. There was considerable yearly variation between cruise dates during any one season. In order to eliminate the effects of short-term shifts in distribution, only cruises spanning approximately similar time periods were used in comparing yearly distribution patterns. The dates and trawl station locations of the cruises considered in this paper are shown in Figures 3 and 4.

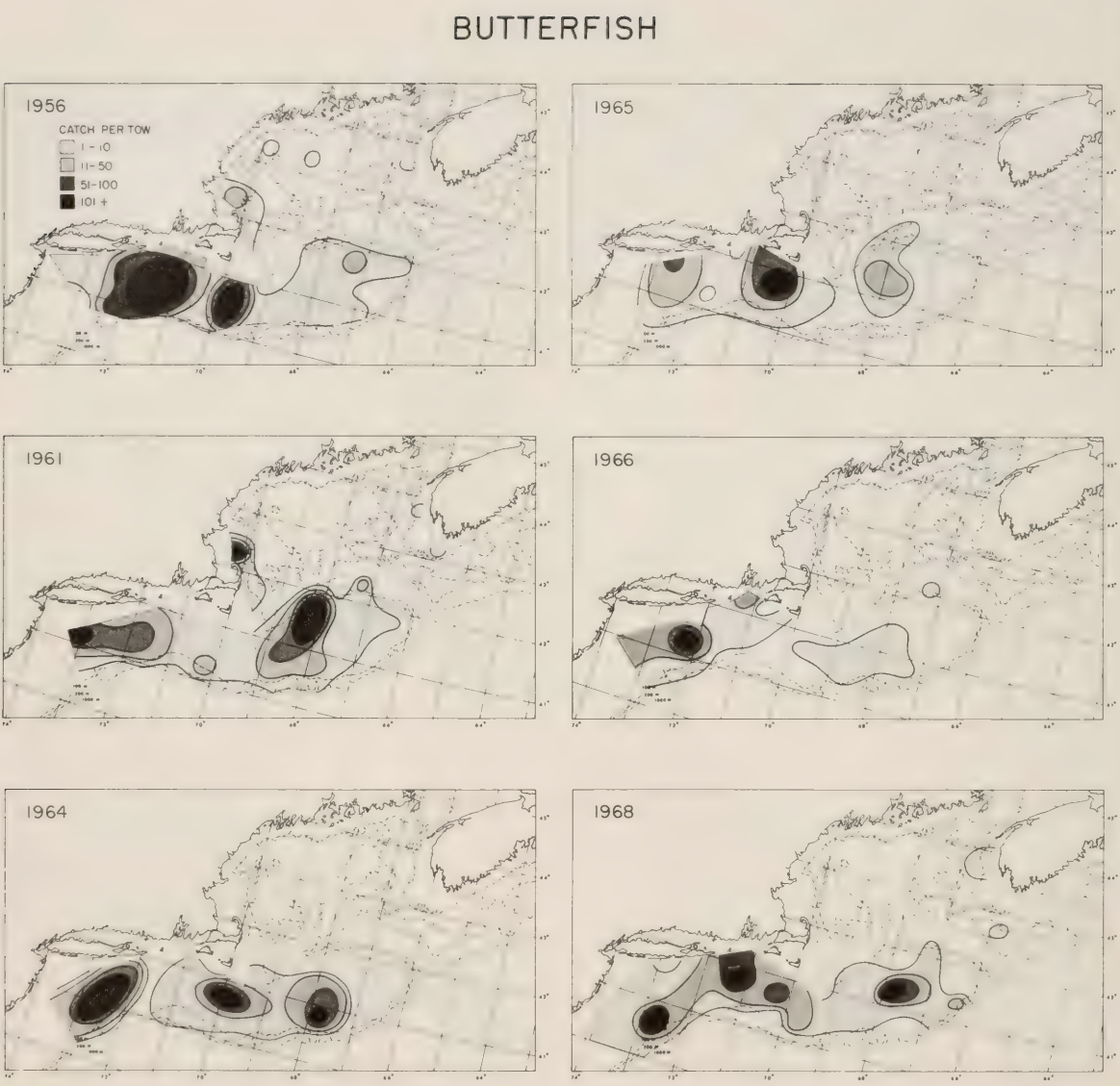

FIGURE 8.—Distribution of butterfish during October-November.

OCTOBER-NOVEMBER DISTRIBUTION

The distribution of American plaice, haddock, yellowtail flounder, and butterfish during October-November 1956, 1961, 1964, 1965, 1966, and 1968 is shown in Figures 5-8.

During 1956, 1961, and 1964, the catches of American plaice were confined to the area north of lat 41°N and east of Cape Cod. In 1965, 1966, and 1968, plaice were found over a much more extensive area. In these years plaice occurred along the southern edge of Georges Bank and off southern New England as far west as long 72°W. The abundance of plaice, as indicated by the average catch per tow, was greater during the latter 3 years.

The catches of haddock were confined to the area east of Nantucket Shoals (long 70°W). The general distribution pattern was similar during all years with the exception that in 1956 (the warmest year) the southern limit of occurrence of haddock was north of its position during the other years. For the most part, the variations in abundance and distribution of haddock between years appear to be related to changes in age composition of the catch due to the predominance of certain year classes. For example, the catches during 1964 and 1965 consisted principally of 1- and 2-year-old fish of the strong 1963 year class (Grosslein, 1969). In general, these young haddock inhabit shoaler water than do older haddock (Colton, 1955).

Although there were marked fluctuations in the abundance of yellowtail flounder between years, there was little change in the general distribution pattern. In all years yellowtail were found in relatively shoal water (<100 m) both to the east and west of Cape Cod. With the possible exception of 1956, the distribution of yellowtail extended considerably beyond the western limit of the sampling area. The bulk of the catch was made south of lat 42°N, although small concentrations occurred off the tip of Cape Cod and on Browns Bank. The greater abundance of yellowtail in later years appears to be due to a succession of strong year classes and not to a major shift in distribution (Lux, 1969).

The main concentrations of butterfish occurred on western Georges Bank and Nantucket Shoals and off southern New England and Long Island. As in the case of the yellowtail, the distribution of butterfish extended beyond the western limit of the sampling area. In 1956 and 1961 only, appreciable numbers of butterfish were caught north of lat 42°N. In these years butterfish occurred just east of Cape Cod, in the Stellwagen Bank area, and in scattered concentrations within the Gulf of Maine. Butterfish were least abundant in 1966. In this, the coldest year, few fish were taken east of Nantucket Shoals.

JULY-AUGUST DISTRIBUTION

The distribution of American plaice, haddock, yellowtail flounder, and butterfish during July-August 1950, 1963, 1964, and 1965 is shown in Figures 9 and 10.

The area of occurrence of plaice extended farther south and west with succeeding years and decreasing temperatures. The catches of haddock were confined for the most part to the area east of Nantucket Shoals, and there was little change in distribution between years. The similarity of the distribution patterns of haddock during July-August and October-November 1964 and 1965 indicates limited seasonal movement. Little change was evident in the general distribution patterns of yellowtail between years. As in the case of the haddock, the similarity of the distribution patterns during July-August and October-November 1964 and 1965 indicates little seasonal movement. There were no marked differences in the distribution of butterfish in these years, although butterfish were least abundant on Georges Bank in 1965, and 1950 was the only year in which appreciable numbers were taken in Cape Cod Bay. In contrast to October-November, the distribution of butterfish during July-August 1964 and 1965 was confined within the western limits of the sampling area.

SEASONAL DISTRIBUTION

Of the four species considered in this paper, only the American plaice and the butterfish showed any appreciable change in distribution coincident with the downward trend in temperature. During both summer and fall there was an extension of the southern and western limits of the area of occurrence of plaice and a contraction of the northern and eastern limits of the area of occurrence of butterfish. Data obtained on cruises made during January-February 1964 and 1966, together with data collected during July-August and October-November 1964 and 1965 (Figures 11 and 12), give evidence of the seasonal distribution of these two species.

Although there were no extensive seasonal changes in the distribution of plaice, the southwesterly extent of the distribution boundaries tended to be greatest during January-February and least during October-November (Figure

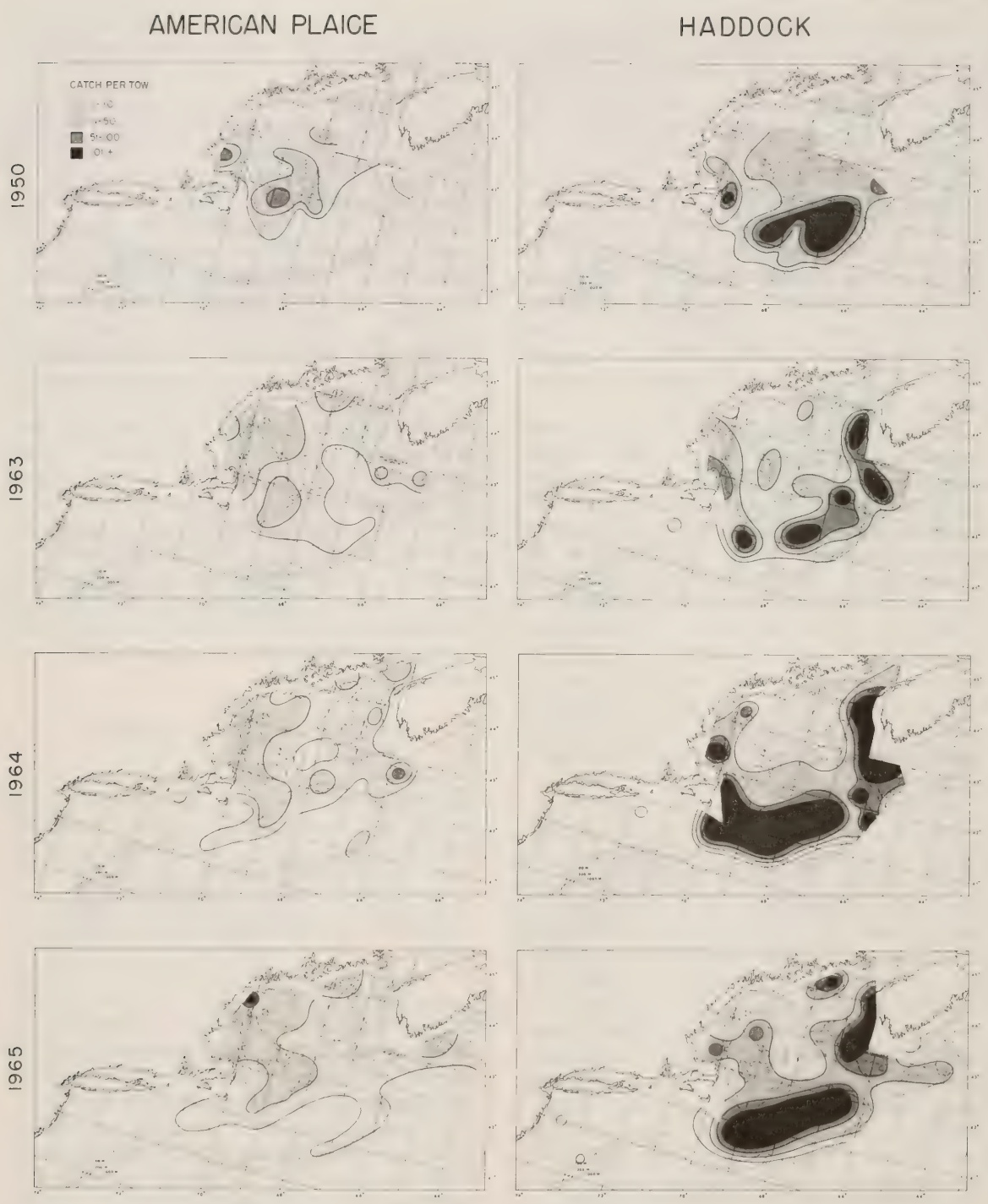

FIGURE 9.—Distribution of American plaice and haddock during July-August.

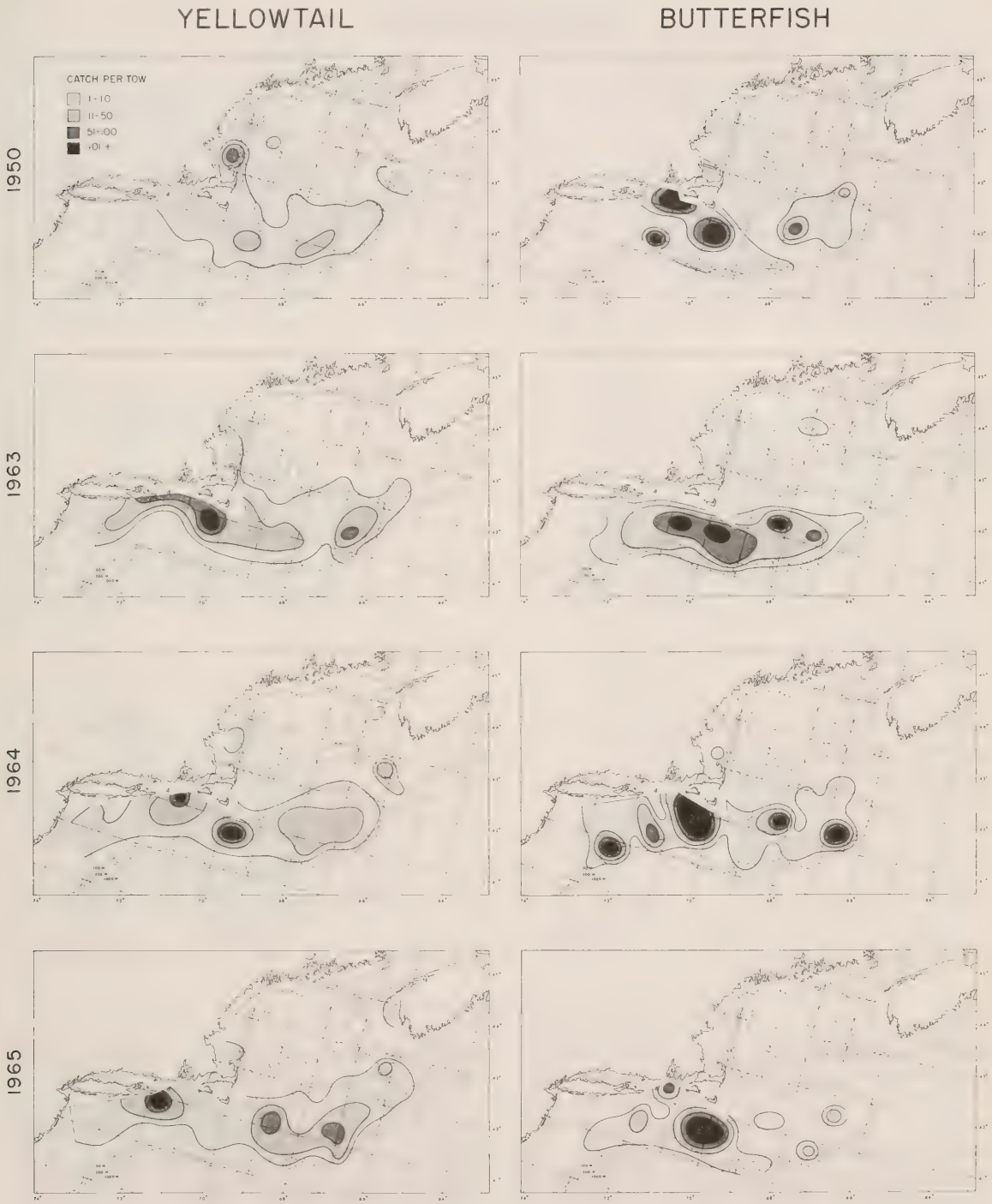

FIGURE 10.—Distribution of yellowtail flounder and butterfish during July-August.

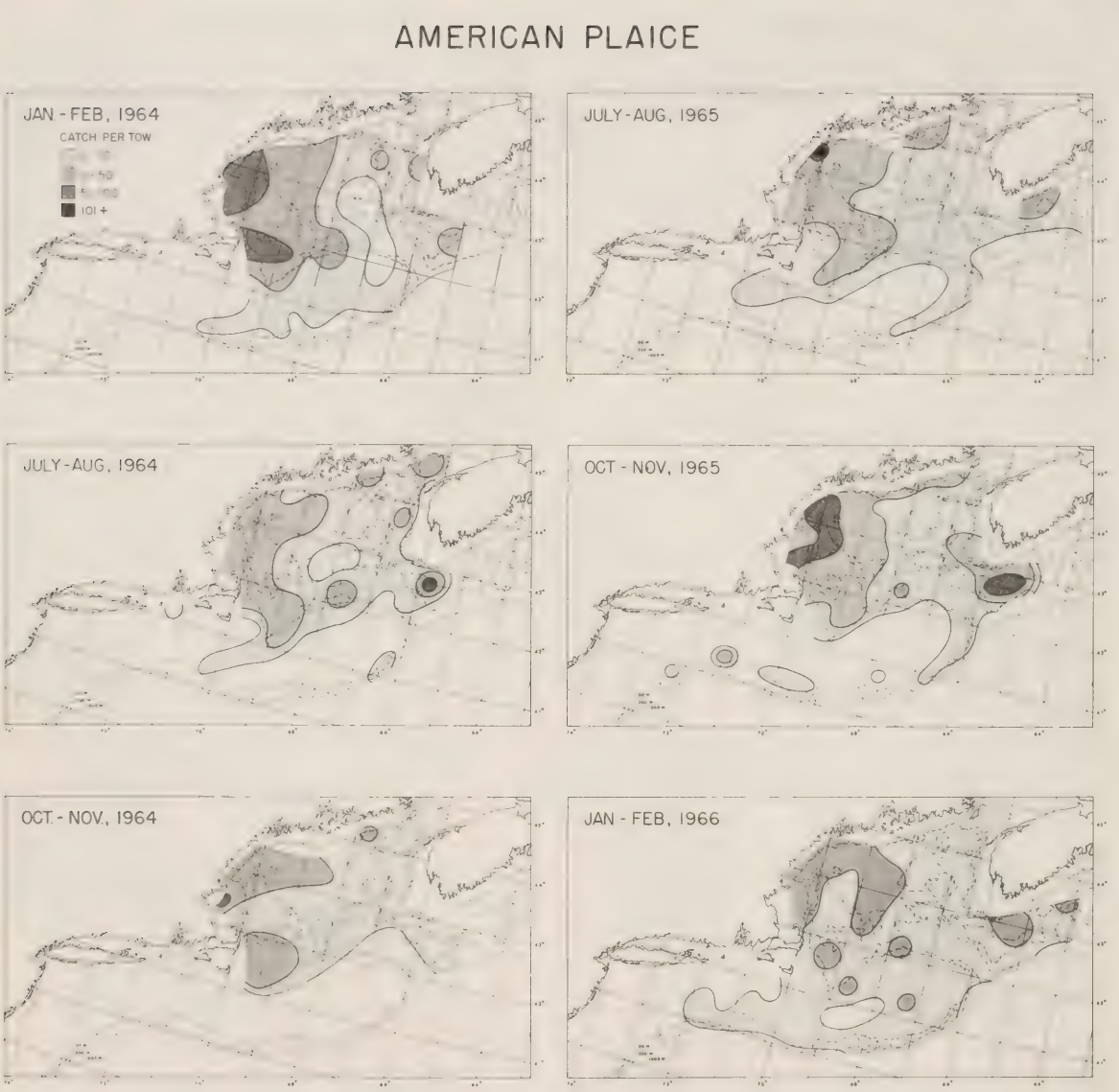

FIGURE 11.—Seasonal distribution of American plaice.

11). In addition, it was only during January-February that plaice were caught in the shoal-water areas of Georges Bank. This seasonal shift in distribution appears to be associated with temperature change. The seasonal maximum and minimum bottom-water temperatures at the depths most frequented by plaice (30-200 m) occur during October-November and February-March respectively (Colton, 1968a; Colton and Stoddard, In press). Bottom-water temperatures over the shoal-water areas of Georges Bank are appreciably higher than those along its periphery during the summer and fall while in the winter and spring the reverse situation exists.

There were no appreciable changes in the dis-

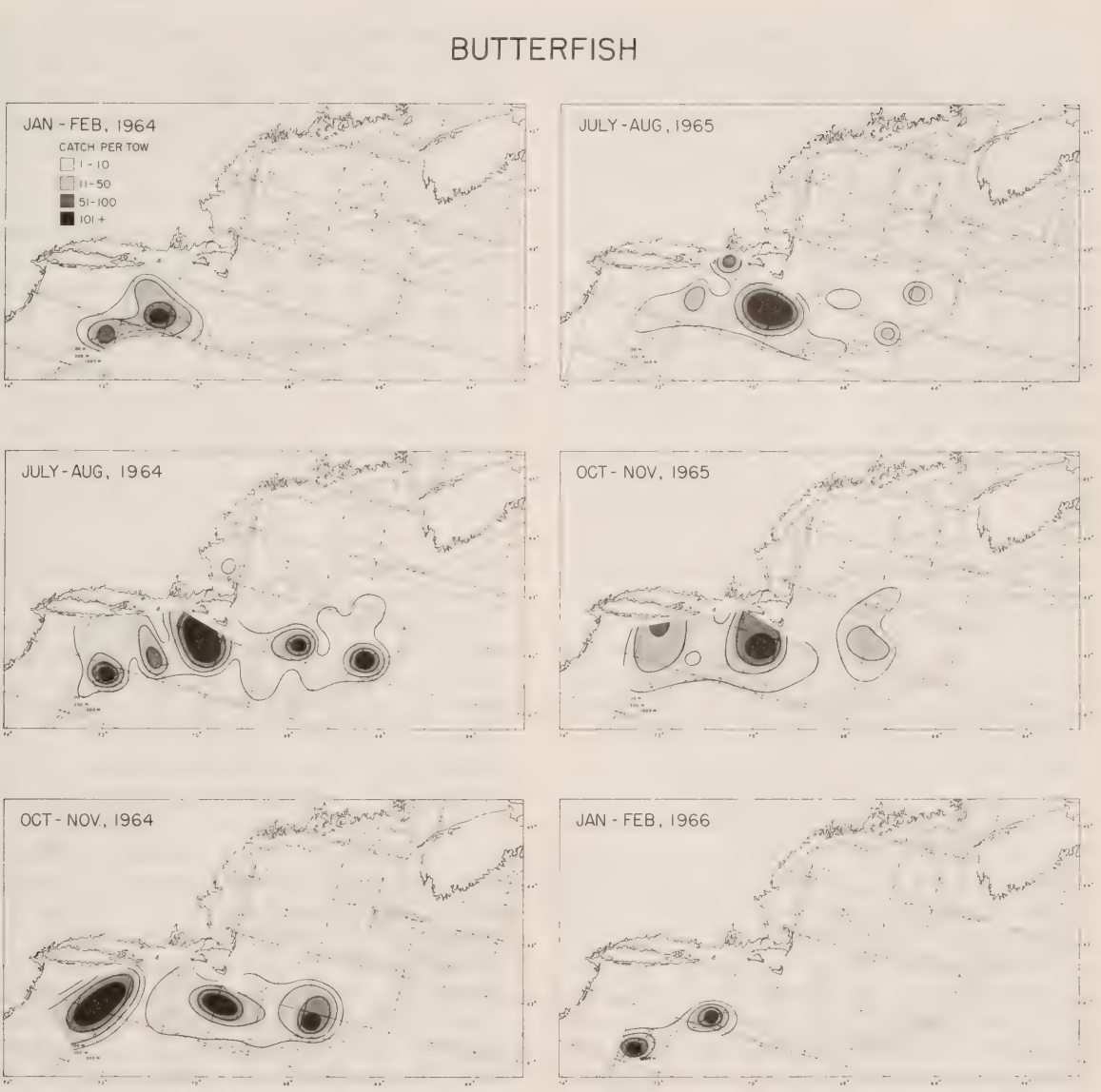

FIGURE 12.—Seasonal distribution of butterfish.

tribution of butterfish between July-August and October-November (Figure 12). However, the fact that the distribution during October-November extended beyond the western limits of the sampling area indicates that butterfish begin their offshore migration from New England coastal waters at this time. By January-February the offshore migration was completed and butterfish were only found in deep water in the southwest corner of the sampling area.

DISCUSSION

A seasonal cold-water temperature barrier in the region of Cape Cod and Nantucket Shoals separates the coastal waters of the Gulf of Maine and the Middle Atlantic Bight from the end of

June to the end of September (Bigelow, 1927; Parr, 1933). This barrier is marked by the presence of a surface pool of cold upwelled water. At other seasons of the year there is open continuity between coastal temperature conditions north and south of Cape Cod. This temperature barrier coincides with the poleward and equatorward boundaries of many species of marine fauna, both pelagic and benthic (Bigelow and Sears, 1939; Parker, 1948; Fritz, 1965; Schopf, 1965).

The seasonal ranges of surface- and bottom-water temperatures in most areas within the Gulf of Maine are less extreme than those characteristic of the Middle Atlantic Bight. The seasonal range of temperature in the shoal-water area of Georges Bank, however, is as great as that at similar depths in the area between Nantucket Shoals and New Jersey (Colton and Stoddard, 1972 and In press). Parr (1933) has described the ecological relationships between homothermal and heterothermal regions separated by a seasonal temperature barrier and has discussed the effect that these contrasting temperature regimes have on the period, extent, and character of the migratory activities of shallow-water fish populations. There is a marked seasonal alternation in the composition of the fish fauna of the Middle Atlantic Bight. In summer this area contains a very rich population of southern migratory fishes which follow the northward dispersal of isotherms as far north as Cape Cod. Winter temperature conditions compel this population to vacate the area, and it is replaced to a considerable extent by northern species, such as herring and cod, which at this season have free access to penetrate as far south as the neighborhood of Cape Hatteras. Although there is no thermal barrier during the winter, the qualitative composition of the fish fauna is not uniform from north to south around Cape Cod. As Parr (1933) has pointed out, this seasonal diffusion of northern populations into areas where no significant temperature differences exist is distinguishable in both its character and effects from the northerly and southerly migrations of complete populations such as occur under thermal compulsion within the Middle Atlantic Bight. In contrast to the Middle Atlantic Bight which contains very few permanent residents, the bulk of the fish fauna in the Gulf of Maine are endemic to the area and there is little seasonal alternation in species composition.

Hutchins (1947) recognized four basic types of temperature zonation which depend on maximum and minimum temperatures critical for survival and repopulation. With the exception of estuarine species such as the green crab which may be subject to winter kill, the distribution of benthic organisms in the area off New England appears to be controlled by summer rather than winter temperatures (Hutchins, 1947; Schopf, 1967). The equatorward boundary of potentially southward-migratory forms is limited by summer temperatures too high for survival and the poleward boundary of northward-migratory forms by summer temperatures too low for reproduction (type 3 of Hutchins, 1947). This is in agreement with the assumption of Hutchins (1947) that at localities having a temperature barrier at only one season (summer at Cape Cod), all distributions terminating there are associated with that barrier.

It is difficult to categorize fish species by strict temperature zonation characteristics. Fish do not have built-in integrators and so must react to prevailing rather than to average conditions. Unlike many benthic invertebrates, fish are able to make short-term excursions and are not dependent solely on passive migrations. It should also be stressed that the distribution within the broad limits set by temperature extremes for survival and reproduction is controlled to some extent by other factors such as food supply (Blackburn, 1969) and substrate conditions (Bigelow and Schroeder, 1953). Of the species considered in this paper, only the American plaice and the butterfish exhibited the expected response to cooling, e.g., extension of the southern range of northern endemic forms and diminution of the northern range of southern migrants.

The butterfish is the only species considered which shows a sensitivity to small changes in temperature and which migrates under the thermal compulsion. Ripe butterfish are taken

throughout their entire range (Caldwell, 1961). In the Gulf of Maine spawning occurs from June through August (Bigelow and Schroeder, 1953). In general, the first arrivals at any point along the coast are in spawning condition, and it would appear that the summer poleward boundary is governed by the minimum temperature suitable for reproduction. Although one can only generalize as to temperature dependence, the timing of arrival of butterfish at various points along the coast of New England and the Maritime Provinces suggests that the minimum spawning temperature is approximately 15°C. The time at which butterfish leave the coastal waters and their distribution in deep water along the continental slope during the winter months indicate a minimum temperature for survival of about 10°C. These temperature approximations are based on average values given by Colton and Stoddard (1972 and In press).

Bigelow and Schroeder (1953) state that the American plaice spawns throughout the Gulf of Maine, but principally in water shoaler than 100 m. More recent observations (Marak and Colton, 1961; Marak, Colton, and Foster, 1962; Marak, Colton, Foster, and Miller, 1962) confirm that the plaice has no well-defined spawning area, although plaice eggs were most abundant in the western Gulf of Maine and over the southeastern part of Georges Bank. Plaice spawn from March through May (Bigelow and Schroeder, 1953). Long-term temperature data in the areas of maximum spawning (Colton and Stoddard, In press) suggest an optimum spawning temperature of 3°-6°C. During the spawning period such bottom-water temperature conditions prevail over most of the area within the 100-m isobath from Cape Cod to New Jersey. Thus, the equatorward boundary of plaice appears to be limited by summer and fall temperatures too high for survival rather than temperatures during the spawning season that are too high for reproduction. As noted previously, plaice were not caught in the Georges Shoal area during the summer and fall. The long-term temperature distribution in this area indicates a maximum temperature for survival of about 12°C. Bigelow and Schroeder (1953) give a range of 10°-13°C as the upper limit of regular occurrence of American plaice.

In contrast to the American plaice, the spawning of haddock is restricted to limited areas within the Gulf of Maine. The most productive spawning grounds are in depths ranging from 40 to 100 m on the northeastern part of Georges Bank and on Browns Bank (Walford, 1938; Bigelow and Schroeder, 1953; Colton and Temple, 1961). Limited and less consistent spawning occurs in the South Channel, Stellwagen Bank, and Jeffreys Ledge areas. Haddock spawn from February through May with the height of spawning occurring on Georges Bank during March and April and on Browns Bank during April and May. Long-term temperature data in the areas of maximum spawning suggest an optimum spawning temperature of 4°-6°C, although spawning does take place at temperatures below and above this range (2°-7°C). There is no evidence that haddock spawn west of Cape Cod, although favorable temperature conditions exist over most of this area during the spawning season.

It is not apparent why haddock select restricted spawning areas, but this limitation may govern in part the extent of their seasonal diffusion into waters west of Cape Cod. Bigelow and Schroeder (1953) give 11°C as the upper temperature limit of the normal range of occurrence of haddock, but the fact that haddock are caught in the Georges Shoal area during the warmest part of the year indicates that haddock can survive temperatures at least as high as 15°C for limited periods. Bottom-water temperatures well below this upper limit occur over much of the area between Cape Cod and Long Island during the summer and fall.

Although seasonal shifts in depth distribution and the timing of spawning of haddock appear to be regulated in part by temperature (Bigelow and Schroeder, 1953; Colton, 1968a), the fact that there was no appreciable change in the geographic distribution of haddock coincident with the downward trend in temperature suggests that factors other than temperature are also critical in the geographic zonation of this species. Bigelow and Schroeder (1953) note that haddock are selective as to substrate type. Haddock avoid areas of rock, kelp, and exceptionally

soft mud and are chiefly caught over broken ground, gravel, pebbles, clay, and smooth hard sand. However, there are no conspicuous differences in the sediments of the Continental shelf east and west of Nantucket Shoals (Uchupi, 1963). Sediments on Georges Bank consist of coarse sand and scattered patches of gravel. In the area between Nantucket Shoals and Hudson Canyon, there is a nearshore zone of silty sand and sandy silt and scattered patches of gravel. Between the 30- and 60-m isobaths is a zone of coarse sand and scattered patches of gravel. From the 60-m isobath to the edge of the shelf, the sediments are similar to those in the basins of the Gulf of Maine and consist of silty sand, sandy silt, and silt.

On a basis of a stomach content analysis of haddock collected on Georges Bank during 1953-54, Wigley (1956) concluded that haddock are exceedingly omnivorous. Their diet consisted principally of sedentary or slow-moving invertebrate animals. The primary food organisms in decreasing order of abundance were crustaceans, mollusks, echinoderms, annelids, and fish. There was considerable variation in dietary components from one location to another. Having no supplementary data on the distribution of benthic fauna, it could not be determined if this variation in diet was related to faunal composition. More recent studies of the distribution of benthic fauna on the continental shelf between Nova Scotia and Long Island (Wigley, 1961; Wigley and McIntyre, 1964; R. L. Wigley—personal communication) show that haddock prefer crustaceans to other food organisms and that the quality and quantity of the benthic fauna to the west of Nantucket Shoals are more than adequate to support a large population of haddock. It is possible that competition for food by the very rich summer and fall populations of such species as the spiny dogfish, silver hake (*Merluccius bilinearis*), and red hake (*Urophycis chuss*) is a factor in restricting the haddock from the Middle Atlantic Bight.

As mentioned previously, the yellowtail flounder is common both to the east and west of Cape Cod at all seasons of the year. Bigelow and Schroeder (1953) observed that the restricted depth range and the nonmigratory habit of this species indicate that yellowtail can tolerate a wide range of temperature. This eurythermic tolerance is further evidenced by the long spawning season and extensive spawning area of this species. The yellowtail breeds over its entire range and from March through August. The spawning period appears to be no later east of Cape Cod than to the west. In addition, Bigelow and Schroeder (1953) noted that individual females evidently spawn over a considerable period of time for only a small part of the eggs ripen simultaneously. The above authors estimated that the yellowtail was subject to a range of temperature from season to season in one part of its area of occurrence or another from about 1° to 12°C. However, the distribution of yellowtail off southern New England and Long Island during the warmest part of the year indicates that they can tolerate temperatures at least as high as 16°C for limited periods.

Yellowtail flounder are only found over sand and sand-mud bottoms and never over rocks, stony ground, and very soft bottom (Bigelow and Schroeder, 1953). This preference for sand sediments is especially evident if one compares the distribution of yellowtail shown in Figures 7 and 10 with the distribution of sediment type shown by Uchupi (1963, Figure 94.1). This predilection for sand sediments is also shown in the data of Fritz (1965, Plates B and 14). It would appear then that except at the extreme northerly and southerly limits of its range, the geographic distribution of yellowtail is more strongly inffuenced by bottom type than by temperature.

It is possible that changes in distribution occurred which were not evident from the survey data due to limitations of sampling and analysis. For example, a number of groundfish species inhabit areas shoaler than that covered by the surveys (<30 m). Among such species is the summer flounder (*Paralichthys dentatus*), which is representative of species restricted for the most part to the area southwest of Cape Cod at all seasons of the year. Pelagic species such as menhaden (*Brevoortia tyrannus*), a warm season migrant having wide fluctuations of occurrence in the Gulf of Maine, and herring (*Clupea harengus harengus*), a boreal species

which ranges as far south as Cape Hatteras in the winter, were not representatively sampled by the otter trawl. Studies undertaken on the distribution of tunas (Blackburn, 1965, 1969) indicate that, in general, pelagic species are much more sensitive to temperature than groundfish species.

There is some evidence to the effect that sensitivity to temperature varies with age of fish. Rollefsen (1949) noted that immature cod can tolerate lower temperatures than mature cod. It is only during the spawning season that appreciable numbers of the older year classes of haddock are caught on Georges Bank (Colton, 1955). In summer these older fish move off into deeper and cooler water, and the Georges Bank population is made up principally of the younger year classes of haddock (1- to 3-year-olds). It would appear that young haddock can withstand higher temperatures than older haddock. The fact that we grouped all age fish in this study may have concealed shifts in distribution associated with specific age-groups.

Any attempt to relate geographic distribution to the direct result of physical processes involves gross oversimplification. It is apparent, however, that there was no major change in the distribution of groundfish coincident with the cooling trend, i.e., the establishment of resident populations south of Cape Cod of species that were formerly winter migrants or a northern diminution of the range of southern migrants. It would appear that the magnitude and rate of temperature change were not sufficient to significantly alter the groundfish composition in the area between Nova Scotia and Long Island. A similar conclusion was reached by Taylor et al. (1957) in their study of changes in the distribution and abundance of marine animals in the same area during a period of warming.

SUMMARY

An alternation in seawater temperature has been observed in coastal and offshore waters in the area between Nova Scotia and Cape Hatteras. There have been a number of reports of southward extensions of range and shifts in distribution of fish and invertebrate fauna during the cooling trend which commenced during 1952-53.

Research vessel survey data is presented to determine what effect the cooling trend has had on the distribution of some important commercial groundfish species in continental shelf waters between Nova Scotia and Long Island. Four species representative of the basic types of geographic zonation characteristic of the area are considered in this paper: American plaice, haddock, yellowtail flounder, and butterfish.

The American plaice and the butterfish showed a change in distribution coincident with the downward trend in temperature, but these shifts were not extensive. During both summer and fall there was an extension of the southern and western limits of the area of occurrence of American plaice and a contraction of the northern and eastern limits of the area of occurrence of butterfish. The equatorward boundary of plaice appears to be limited by summer temperatures too high for survival and the poleward boundary of butterfish by summer temperatures too low for reproduction.

There was no change in the general distribution of haddock and yellowtail flounder. In all years and seasons the catches of haddock were confined for the most part to the area east of Cape Cod. Restricted spawning areas and competition for food may govern, in part, the seasonal diffusion of haddock into waters west of Cape Cod.

Yellowtail flounder occurred both to the east and west of Cape Cod at all seasons. Their distribution was limited to depths shoaler than 100 m and to areas of sand bottom. The restricted depth range, long spawning season, extensive spawning area, and nonmigratory habit of the yellowtail flounder indicate that this species can tolerate a wide range of temperature. It appears that except at the extreme northerly and southerly limits of its range, the geographic distribution of yellowtail flounder is more influenced by bottom type than by temperature.

Although it is possible that changes in distribution did occur which were not evident from the survey data, it appears that the magnitude and rate of temperature change during the cooling period were not sufficient to significantly

alter the distribution of groundfish in the area between Nova Scotia and Long Island.

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WATER TEMPERATURE AND THE MIGRATIONS OF AMERICAN SHAD

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ABSTRACT

The peak of spawning runs of American shad (*Alosa sapidissima*) into rivers at various latitudes on the Atlantic and Pacific coasts of North America takes place when water temperatures are near 18.5°C. At the Bonneville Dam, Columbia River, Wash., 90% of the run as a rule takes place when river temperatures are between 16.0° and 19.5°C. At the fish ladder of the Holyoke Water Power Company on the Connecticut River, the temperature at the peak of the shad run averaged 19.5°C for 15 years. In the St. Johns River, Fla., peak movement occurs in December and January at the time of the annual minimum water temperatures, or 14.0° to 20.0°C.

Migrations of shad in the Atlantic Ocean follow paths associated with approximately the same range of temperatures (13.0°-18.0°C). Annual cycles of ocean warming cause shad to move into the Gulf of Maine in the summer, to the middle Atlantic in the winter, and to the south in the early spring. Juvenile shad move downstream in the fall, coinciding with a decline in the temperature of each stream to below 15.5°C. A path of migration for shad in the Pacific Ocean is hypothesized from the known seasonal changes in ocean temperature. The potential effects of artificial warming of streams on timing and survival of shad runs in northern and southern latitudes is discussed.

The American shad (*Alosa sapidissima*), in spite of declines in abundance on the Atlantic coast of the United States caused by obstruction of spawning runs by dams, by water pollution, and by overfishing, continues to provide a catch each year of some 8 million pounds valued at slightly more than one million dollars to the fishermen (Walburg and Nichols, 1967).

There is as yet no rationally based management scheme to prevent overfishing of shad, and dams and pollution continue to increase. Recent changes in the environment for shad have been brought about by the greatly increased heating of the water by steam-electric generating stations. There will be a further increase in the construction of these facilities; thus the Federal Power Commission in 1960 estimated that by 1980 the generating capacity of hydroelectric power stations would double—some accomplished by construction of dams and some by adding capacity at existing dams—but at the same time, steam-electric capacity would triple (Federal Power Commission, 1960). Other experts regard these estimates as conservative (American Public Power Association, 1960). It therefore becomes pertinent to ask what effects the warming of water may have on fish in streams used for cooling. This paper analyzes the effect of water temperature on the movements of shad in streams and in the ocean.

It is appropriate that this paper, which traces the relationship of migrations of American shad to temperature of the water, should appear in a volume dedicated to Dr. O. Elton Sette. His interest in the effects of temperature on migrations of fishes has been a stimulus to the work of his colleagues for over 30 years. He has always been generous in his encouragement of those around him. In 1957, the Pacific Oceanic Fishery Investigations, of which he was the first Director, began publication of monthly sea-surface temperature charts for the Pacific Ocean as an aid to fishermen and biologists studying fish distribution. The successors of these charts are still being issued by the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla Laboratory. Other scientists and agencies have come to see their utility and popularity and have commenced publication of sea surface temperature charts for other parts of the world.

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The present paper, therefore, owes a great deal to Dr. Sette both in its conception and execution. He conceived that there was a relationship between water temperature and fish distribution, and he stimulated the production of charts to which we are able to refer in order to establish the relationship of shad migrations to water temperature.

SHAD RUNS AND RIVER TEMPERATURE

As early as 1884, Marshall McDonald developed a theory that shad are restricted to a narrow range of temperatures and that the timing of shad runs thus depends on when the water warms. McDonald (1884, p. 599, 604, 605) stated that shad

> ... occupy an hydro-isothermal belt, or area, limited by the temperature of 60° F. to 70° F.; that they move with this belt, *i.e.*, as the season advances, into and up the rivers....
>
> ... In the Savannah River they appear early in January, and in the Neuse River at a period not much later than in the Savannah. In the Albemarle the important Shad seine-fisheries begin early in March, but doubtless the fish are in the Sound some time before that date; not, however, in numbers sufficient to justify the great expenses attendant upon the operation of these large seines. In the Chesapeake Bay they make their appearance in February, although the height of the fishing season in its waters is during April and May, and at a date somewhat later in the more northern tributaries. In the Delaware, Connecticut, Merrimac, and St. John (Nova Scotia) Rivers, Shad are first seen at periods successively later as we proceed farther north. The date of their first appearance in any of these waters, however, varies from season to season, the limit of such variation being from three to four weeks.
>
> These irregularities in the time of the run into our rivers, which cause so much perplexity and discouragement to the fishermen, are, however, readily explained when we keep in view what has been already said in regard to the influences of temperature in determining the movements of these fishes.

McDonald pointed out that the shad run in a particular river may be delayed if the water cools. Although rising temperatures accelerate the run, a sudden increase may also retard it. The downstream migration of the juvenile shad occurs when water temperatures fall to below 60°F (15.5°C).[3] In support of his thesis, McDonald provided a table of daily shad catches and water temperatures in the Potomac River for the year 1881. Shad were caught in water from 8.0° to 24.5°C. We performed a frequency analysis of these data which shows that the average shad was associated with a temperature of 18.5°C. Ninety percent of the run took place between 12.0° and 21.0°C. McDonald also supplied a table showing monthly average water temperatures for the St. Johns River, Fla., in 1877 and 1878. He stated that shad first appeared in November when the average temperature was 63.5°F (17.5°C) and that spawning took place in February and March when the average temperatures were 58.0° and 62.2°F (14.5° and 17.0°C). McDonald provided no quantitative data on shad in the St. Johns River, however, and his thesis therefore apparently rests on data from the one year and one river in which both shad catches and water temperatures were available. He gave no data to support his statement on migrations of juveniles.

Working in the field, one readily becomes convinced as did McDonald (1884) that water temperature affects the run of shad. This observation has also been made by Leim (1924), Talbot (1954), and Massmann and Pacheco (1957). The difficulty has been to develop a quantitative measure or prediction of the effect. Talbot (1953), by means of linear regression, analyzed the timing of the shad run in relation to river flow and river temperature at Bonneville Dam on the Columbia River. Temperatures and flows are recorded there, and Talbot had available shad counts made from 1938 to 1950 as the fish ascended the fish ladders at the dam. He concluded that flow and temperature do affect the time of entry of shad into the river, although the correlation coefficient of time of the run and temperature was not quite significant at the 5% level.

Now 19 more years of data are available (Table 1). The 32 years of data show a highly significant partial correlation of temperature, as well as a significant partial correlation of flow, with the timing of the shad run. Of course, this

[3] All temperatures used in developing this paper were originally recorded in Fahrenheit. Our conversions to Celsius have been rounded to the nearest 0.5°C.

TABLE 1.—Time of median shad passage at Bonneville compared with time when temperature exceeded 15.5°C and flow diminished to 325,000 cfs and number of days counted from May 31 (shown in parentheses).[1]

Year	Date on which: Half of shad were counted	Temperature rose above 15.5°C	Flow decreased to 325,000 cfs
1938	July 24 (54)	June 24 (24)	July 17 (47)
1939	July 7 (37)	June 26 (26)	June 12 (12)
1940	June 30 (30)	June 9 (9)	June 16 (16)
1941	July 5 (35)	June 5 (5)	May 30 (—1)
1942	July 21 (51)	June 28 (28)	July 1 (31)
1943	July 20 (50)	June 29 (29)	July 24 (54)
1944	July 17 (47)	June 21 (21)	June 21 (21)
1945	July 13 (43)	June 18 (18)	July 4 (34)
1946	July 8 (38)	June 29 (29)	July 13 (43)
1947	July 4 (34)	June 16 (16)	July 4 (34)
1948	July 18 (48)	July 19 (49)	July 13 (43)
1949	July 11 (41)	July 13 (43)	June 22 (22)
1950	July 21 (51)	July 7 (37)	July 28 (58)
1951	July 8 (38)	June 16 (16)	July 25 (55)
1952	July 15 (45)	June 21 (21)	July 8 (38)
1953	July 15 (45)	June 30 (30)	July 20 (50)
1954	July 25 (55)	July 7 (37)	July 30 (60)
1955	July 23 (53)	July 12 (42)	July 29 (59)
1956	July 14 (44)	June 29 (29)	July 15 (45)
1957	July 11 (41)	June 20 (20)	July 25 (55)
1958	July 7 (37)	May 30 (—1)	July 28 (58)
1959	July 17 (47)	June 22 (22)	July 18 (48)
1960	July 5 (35)	June 4 (4)	July 12 (42)
1961	July 7 (37)	June 16 (16)	July 4 (34)
1962	July 13 (43)	June 15 (15)	July 29 (59)
1963	July 8 (38)	June 13 (13)	July 1 (31)
1964	July 14 (44)	June 29 (29)	July 24 (54)
1965	July 1 (31)	June 23 (23)	July 14 (44)
1966	July 8 (38)	July 16 (46)	July 19 (49)
1967	July 12 (42)	June 21 (21)	July 17 (47)
1968	July 3 (33)	June 12 (12)	July 1 (31)
1969	June 21 (21)	June 3 (3)	June 19 (19)

Shad-temperature partial correlation $r = 0.58$, $P<0.01$
Shad-flow partial correlation $r = 0.44$, $P<0.05$
Temperature-flow partial correlation $r = -0.004$ not sig., df = 29

[1] Method is that of Talbot (1953) as are data 1938-1950, data 1951-1969 from Corps of Engineers (1951-1969).

analysis suffers from the usual defects of data on two or more factors which may trend in the same direction without necessarily being related in a cause-and-effect manner. For example, we do not believe that the significant correlation of flow and the timing of the runs has any particular meaning beyond the fact that the shad run occurs after flows begin to decline. Shad migrate into streams of various sizes, and we do not think that they select a particular flow in a particular stream. On the other hand, the fact that they select the same water temperature in different streams and, as will be shown later, that in their oceanic migration they remain in water of the same temperature points to the conclusion that the timing of the shad run is related to water temperature.

To find the particular temperature preferred by shad, we tabulated the temperature when each fish was counted at the Bonneville fish ladders. For each year we then calculated an average of these temperatures. This amounts to determining the temperature at the peak of the shad run (Table 2). Such a procedure is justified by the large samples and the fact that the frequency distribution is approximately normal. Very little variation in the temperature at the peak of the run occurred from year to year. Most of the time the peak occurred at 18.0°C. In 78% of the years the peak appeared in the range 16.5° to 19.0°C. (Table 3). In the average year, 90% of the shad run was counted when the temperatures ranged between 15.5° and 19.5°C. In 26 of the 32 years the temperature varied only 4.0°C or less during the time when 90%

TABLE 2.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad counted at Bonneville Dam fishways,[1] Columbia River.

Year	Lower	Peak	Upper	Difference
1938	17.0	19.5	21.5	4.5
1939	15.0	17.0	21.0	6.0
1940	17.0	19.0	20.0	3.0
1941	17.0	20.0	23.0	6.0
1942	17.0	19.5	21.0	4.0
1943	16.0	18.0	19.0	3.0
1944	17.0	14.0	21.0	4.0
1945	18.0	19.5	20.5	2.5
1946	15.0	16.5	19.0	4.0
1947	16.0	18.0	19.5	3.5
1948	17.0	19.5	20.5	3.5
1949	13.5	15.5	16.5	3.0
1950	16.5	18.0	19.0	2.5
1951	15.5	17.0	19.0	3.5
1952	15.5	18.5	19.5	4.0
1953	16.5	18.5	19.0	2.5
1954	15.0	16.5	18.0	3.0
1955	14.5	17.0	19.0	4.5
1956	16.0	18.5	20.0	4.0
1957	15.5	18.5	20.0	4.5
1958	18.5	20.0	22.0	3.5
1959	16.5	18.5	20.0	3.5
1960	15.0	18.0	20.0	5.0
1961	16.5	18.5	20.5	4.0
1962	16.5	18.0	20.0	3.5
1963	16.0	18.0	19.0	3.0
1964	15.5	18.0	19.0	3.5
1965	16.0	18.0	19.5	3.5
1966	15.0	16.5	19.0	4.0
1967	17.0	18.5	19.5	2.5
1968	15.5	16.5	19.0	3.5
1969	16.0	18.0	19.0	3.0
Mean	16.0	18.0	19.5	3.5

[1] From Corps of Engineers (1948-1969) and unpublished data for which we are indebted to Ivan Donaldson, Corps of Engineers, and Kingsley G. Weber, National Marine Fisheries Service.

TABLE 3.—Number of years when given temperature was recorded at the peak of the spawning run.

Temperature at peak (°C)	Number of years	Percentage of years
15.5	1	3
16.0	0	
16.5	4	78
17.0	3	
18.0	9	
18.5	7	
19.0	2	
19.5	4	19
20.0	2	

TABLE 4.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad counted at Holyoke Water Power Company fishway, Connecticut River.

Year	Lower	Peak	Upper	Difference
1955	19.0	19.5	23.5	4.5
1956	19.0	21.0	23.0	4.0
1957	18.5	19.5	22.5	4.0
1958	16.0	18.5	18.5	2.5
1959	17.0	20.5	23.0	6.0
1960	15.5	19.5	20.0	4.5
1961	15.0	18.5	21.5	6.5
1962	16.0	20.5	21.0	5.0
1963	16.5	20.0	21.5	5.0
1964	16.0	19.5	20.5	4.5
1965	16.5	19.0	21.5	5.0
1966	17.0	19.5	21.0	4.0
1967	16.5	20.0	23.0	6.5
1968	14.5	17.0	21.5	7.0
1969	16.5	19.0	22.0	5.5
Mean	16.5	19.5	21.5	5.0

of the shad appeared at the Bonneville fish ladders. In only 3 years did the range exceed 4.5°C (Table 2).

The only comparable data that we have been able to locate on the Atlantic coast concern the shad passed by the fish lift of the Holyoke Water Power Company located 138 km from the mouth of the Connecticut River. Daily records of water temperature and the number of fish lifted over the dam show that few shad were passed when the water temperature was below 14.0°C. Peak passage occurred at temperatures ranging from 16.5° to 21.5°C (Table 4). This compares closely with the temperature of peak shad passage (16.5°-19.0°C) at Bonneville Dam, 233 km from the mouth of the Columbia River.

Commercial catches provide less direct, and therefore less reliable, data on the timing of shad runs. These can be affected by many extraneous factors such as market price, which leads to heavier sampling in the early part of the run, and turbidity of the water, which would have the same effect because catch per effort would be higher early when turbidity is high. Nevertheless, the temperatures found to be associated with peak commercial catches are in general agreement with those associated with actual counts at the fishways.

For the St. Johns River, Fla., mean weekly shad catches (in pounds) were calculated from daily catch records of the Morris Crab Company for the years 1962 to 1967. These are plotted in Figure 1 with mean monthly river temperatures developed from daily temperature records of the Florida Light and Power Company for the years 1960 to 1967. Fishing effort was approximately equal from day to day and year to year from mid-November to mid-March, but after this time market fluctuations resulted in sporadic fishing effort. In order to eliminate error resulting from sporadic fishing effort, catches made after mid-March were omitted from the analysis.

Shad migrations in the St. Johns River corresponded closely to the period of lowest annual river temperatures, confirming the earlier observations of McDonald (1884). Few, if any, shad entered the river at temperatures in excess of 20.0°C prior to mid-November, and peak numbers occurred in mid-January when temperatures were at the annual low (15.0°C). As temperatures increased, in February and March, the relative abundance of shad declined.

Massmann and Pacheco (1957) investigated the relationship between temperature and shad catch in the York River, Va., in the years 1953 to 1956. From their data we calculated the mean catch of shad per net day, by weekly intervals, February 15 to June 1. The relationship between the timing of shad migrations in the York River and mean monthly river temperatures (developed from daily records for the period 1953 to 1962 that were supplied by the Virginia Institute of Marine Science) is illustrated in Fig-

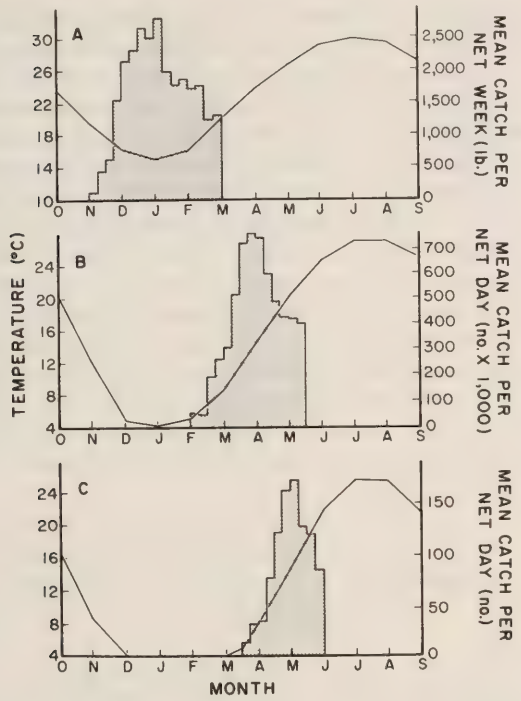

FIGURE 1.—Shad catches at various temperatures in three Atlantic coast rivers. (A) St. Johns River, Fla.—temperatures are averages, 1960-1967; shad catches in pounds are from weekly catches of the Morris Crab Company, 1962-1967. (B) York River, Va.—temperatures are averages, 1953-1962; shad catches are numbers per net day, 1953-1956 (Massmann and Pacheco, 1957). (C) Connecticut River, Conn.—temperatures are averages, 1958-1969; shad catches are numbers per net day, 1944-1964 (courtesy Angelo Baldi) and 1965-1969 (Leggett, 1969).

ure 1. Few, if any, shad entered the York River until late January when river temperatures exceeded 4.0°C, and peak numbers were captured in April at temperatures around 14°C. At higher temperatures catches declined.

For the Connecticut River the mean catch of shad per net day, by weekly intervals, April 1 to June 15, was estimated from the daily catch records of commercial fisherman Angelo Baldi for the period 1944 to 1964, and from the daily records of shad captured for tagging by biologists of the Essex Marine Laboratory from 1965 to 1969. These data are presented in Figure 1, together with mean weekly river temperatures developed from daily water temperature records of the Hartford Electric Light Company, and Essex Marine Laboratory for the period 1958 to 1969. Shad are generally soft-bodied and of little economic value after mid-June; from then on fishing effort is much reduced and is more sporadic. For this reason, the histogram of mean weekly catch was terminated in mid-June. Shad first entered the Connecticut River from late March to early April when water temperatures ranged from 4.0° to 6.0°C. The mean weekly catch increased with temperature until mid-May when temperatures averaged about 15°C. Catches declined steadily at higher temperatures. During the period for which accurate daily temperature records were available, 1958 to 1969, the mean temperature at which the peak catch was obtained at the mouth of the river was 13.0°C (Table 5). In 10 out of 12 of those years, the peak catch occurred at temperatures between 11.0° and 15.5°C. In the Connecticut River, a large sport fishery for shad operates at Enfield, in the area 88 to 109 km from the river mouth. A daily record of the number of anglers and the number of shad caught in a State-controlled fishing area has been maintained since 1942. A daily record of the water temperature at the fishing area has also been kept. Most shad were caught by angling at temperatures ranging from 11° to 18°C (Table 6). On the average, the peak occurred near 15°C. As noted previously, the temperature of peak shad passage at Holyoke, 29 km farther upriver, occurred at temperatures averaging 19.5°C and ranging from 16.5° to 21.5°C.

TABLE 5.—Water temperature (°C) associated with peak of shad catch and upper and lower temperatures associated with middle 90% of the catch at Saybrook, Conn.

Year	Lower	Peak	Upper	Difference
1958	8.5	11.5	19.0	10.5
1959	6.0	13.5	22.0	16.0
1960	10.0	15.5	20.0	10.0
1961	10.5	13.5	16.5	6.0
1962	12.5	14.5	22.0	9.0
1963	10.0	14.5	20.5	10.5
1964	8.0	13.5	18.5	10.5
1965	8.5	14.0	20.0	11.5
1966	8.5	9.5	13.0	4.5
1967	6.5	9.5	13.5	7.0
1968	12.0	13.0	16.5	4.5
1969	8.5	11.0	14.5	6.0
Mean	9.0	13.0	18.0	9.5

TABLE 6.—Water temperatures (°C) associated with the peak of the shad run and lower and upper temperatures associated with the middle 90% of the shad caught by anglers at Enfield, Conn.

Year	Lower	Peak	Upper	Difference
1953	8.0	12.0	16.5	8.5
1954	8.0	10.5	14.0	6.0
1955	15.5	18.0	18.0	2.5
1956	11.0	14.5	18.0	7.0
1957	14.0	16.0	18.0	4.0
1958	11.0	16.0	17.5	6.5
1959	14.0	18.5	18.5	4.5
1960	14.0	16.0	20.5	6.5
1961	9.0	14.0	16.5	7.5
1962	8.5	16.0	21.0	12.5
1963	12.0	16.5	16.5	4.5
1964	11.5	17.0	18.5	7.0
1965	11.5	17.0	23.0	11.5
1966	9.0	15.0	18.5	9.5
1967	8.0	13.5	20.0	12.0
1968	11.0	15.0	15.5	4.5
1969	11.5	14.5	18.5	7.0
Mean	11.0	15.5	18.0	7.0

TABLE 7.—Water temperatures and counts per hour of downstream migrating juvenile shad at Matamoras, Pa., September and October 1951. (From Sykes and Lehman, 1957.)

Date		Temperature °C	Shad per hour
September	10	20.5	5
	17	20.5	0
	21	20.5	1
	24	21.0	0
	28	20.0	10
	29	18.0	20
	30	14.0	65
October	1	17.0	59
	5	21.0	0
	8	14.0	600
	9	14.0	600
	10	15.0	300
	13	15.0	350
	14	14.0	350
	15	14.0	70
	16	14.0	10
	17	15.5	0
	19	15.0	0
	29	15.0	0

As these data clearly show, the timing of shad spawning migrations is highly correlated with specific water temperatures in all three of the rivers studied. Most shad entered these rivers when temperatures were between 10.0° and 15.0°C, even though this required considerable variation in the timing of shad to changing temperature conditions in the three rivers. In the St. Johns River (Fla.), water temperatures seldom fall below 14.0°C, and the spawning run occurs at about the seasonal temperature minimum in January. These Florida shad must begin to enter the river during conditions of declining water temperatures, as opposed to the shad from the York and Connecticut Rivers which begin their migrations as temperatures are increasing above an apparent lower limit of 4.0°C. In Florida, most of the migration occurs while river temperatures are below 20.0°C. Maximum movements of shad into the York and Connecticut Rivers occur at temperatures of about 15.0°C. The sporadic nature of fishing effort late in the runs when temperatures were higher probably leads to an underestimate of temperatures, but in all three rivers the mean weekly catch at 19.0° to 21°C was approximately one-half that recorded at 13.0° to 15.0°C.

TIMING OF OUTMIGRATION OF JUVENILES RELATED TO STREAM TEMPERATURE

Juvenile shad normally spend their first summer in the river in which they were spawned. They begin to move downstream to the sea in the fall. This migration, too, is apparently triggered by temperature. Sykes and Lehman (1957) provided the interesting quantitative data in Table 7. The largest number of shad moved downstream when the temperature dropped below 15.5°C for a period of several days. Similar findings were reported by Smith (1899), Walburg and Nichols (1967), and Chittenden (1969).

OCEANIC WATER TEMPERATURES ASSOCIATED WITH SHAD MIGRATIONS

Talbot and Sykes (1958) were the first to describe the oceanic migrations of shad. From 19 years of tagging by the U.S. Fish and Wildlife Service, they learned that shad from all the major Atlantic coast rivers congregate in the Gulf of Maine in the summer and fall. This group of shad includes immature fish from all streams and survivors of spawning from streams north of Chesapeake Bay. South of Chesapeake Bay there are no survivors after spawning. Talbot

and Sykes believed that the shad move south to waters off the Middle Atlantic States in the winter. However, they had only one recapture in December. In January or February shad do begin to appear off the central Atlantic Coast from North Carolina to Long Island. Confirmation of the conclusions of Talbot and Sykes (1958) came from Walburg and Nichols (1967) who reported 49 shad caught at lat 40°N, long 70°41'W (Point A, Figure 2A), January 23 to February 2, 1961, by the research vessel *Delaware*. If mature in the spring, the shad then move either north or south to their home streams and spawn. The shad runs in southern streams occur early in the spring and progressively later northward.

One of us (Leggett) has conducted extensive tagging studies of Connecticut River shad since 1965. From 1965 to 1969, 18,374 mature shad were marked and released in the lower Connecticut River. In all, 83 of these shad have been recovered along the Atlantic coast from North Carolina to the Bay of Fundy, 66 with complete information as to date and place of recapture. Over 300 shad were recovered in the lower Connecticut River 1 year or more after tagging. These recaptures, together with coastal recoveries from 4,500 shad tagged by the U.S. Bureau of Fisheries and U.S. Fish and Wildlife Service between 1938 and 1949, were plotted on monthly surface temperature charts of the western Atlantic Ocean (U.S. Naval Oceanographic Office, 1967; U.S. Coast Guard Oceanographic Unit,

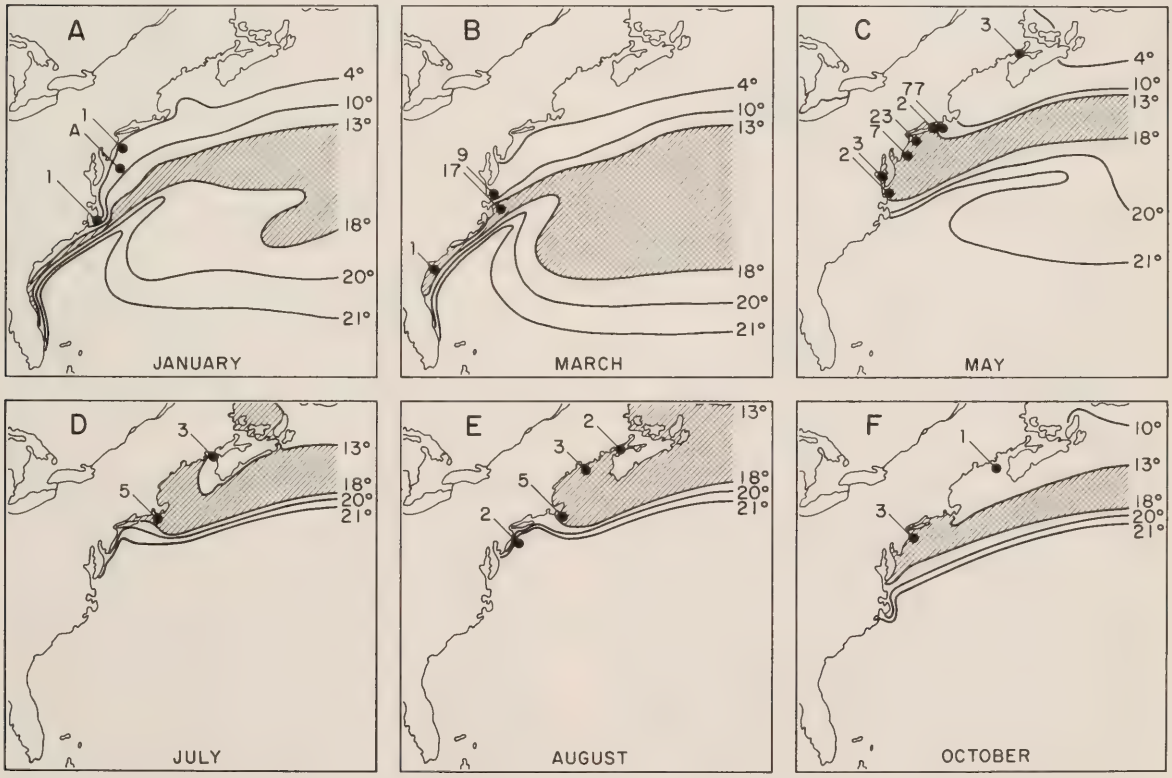

FIGURE 2.—Atlantic Ocean average sea surface temperatures and associated locations of shad recaptures for selected months. Number of recaptures is shown. Point A represents the 49 shad Walburg and Nichols (1967) reported caught in a trawl. (Temperature charts adapted from U.S. Naval Oceanographic Office, 1967; inshore segments of isotherms were refined with the aid of surface temperature charts by U.S. Coast Guard Oceanographic Unit, 1969-1971, see footnote 4.)

1969-1971).[4] Their distribution in time and space corresponds closely to the position of the 13° to 18°C isotherms. Six of these charts are presented in Figure 2.

In July, August, and September, the 13° to 18°C isotherms are situated in the Gulf of Maine (Cape Cod to Bay of Fundy). It was from here that Talbot and Sykes (1958) reported the majority of their recoveries in these months. Recoveries from the Connecticut River taggings were confined exclusively to this area during July (Figure 2D), August (Figure 2E), and September. In October (Figure 2F), November, and December these waters cool and the 13° to 18°C isotherms move south to the middle Atlantic region, the general area where shad are said to winter (Talbot and Sykes, 1958; Walburg and Nichols, 1967). During these months, as stream temperatures drop below 15.5°C, juvenile shad migrate out of their streams and, as Talbot and Sykes suggested, they probably join the large body of southward migrating adult and immature shad as they pass on their way to the middle Atlantic wintering area.

In December and January (Figure 2A), water of appropriate temperature extends in a narrow band near the coast of Florida, and the shad can move into the St. Johns River along the band. In February and March (Figure 2B), 13° to 18°C water bathes the coast of the southern Atlantic States from Cape Hatteras south providing access for shad to coastal streams in those States. At this time Connecticut River shad first appear off the coast of North Carolina and Virginia and begin to move north along the coast, mainly within the bounds of the 13° to 18°C isotherms. During April and May (Figure 2C), shad continue to move north as they follow the movement of the 13° to 18°C isotherms. In April they are located around Chesapeake Bay and Delaware Bay and contribute to the runs into streams in these areas. By May shad are concentrated in the Long Island region and run into the Hudson and Connecticut Rivers. In June there is movement of the isotherms farther north along the coast, corresponding to the peaks of the shad runs in streams to the north. Again in July (Figure 2D), August (Figure 2E), and September, the Gulf of Maine reaches optimum temperature for the species.

The northern and southern limits of the range of shad on the Atlantic coast appear to be defined by the temperature relationship described above. In June and July a narrow tongue of 13°C water typically extends to the mouth of the St. Lawrence River, the northern extension of the fish's range. North of the St. Lawrence, the ocean seldom warms above 13°C. In the south shad appear to be blocked from extending their range into the Gulf of Mexico by a band of water south of Cape Kennedy that rarely cools below 21°C even in December and January (U.S. Naval Oceanographic Office, 1967). It is probable that *Alosa alabamae*, a closely related species that is native to most principal streams tributary to the Gulf of Mexico east of the Mississippi, evolved from *Alosa sapidissima*. Prior to the emergence of the Florida peninsula, the range of shad may have included these Gulf rivers. Florida's emergence would have produced an effective geological barrier between the stocks, thereby promoting their separate evolution. In this connection we note that a narrow band of water of the temperature range 13° to 18°C extends along the northernmost coast of the Gulf of Mexico during the months of December to March (Rivas, 1968).

PACIFIC OCEAN MIGRATION OF SHAD

Prior to 1871 shad occurred only on the eastern coast of North America. In that year shad from eastern rivers were stocked in the Sacramento River. So successful was the venture that by 1880 shad were reported to range from Todos Santos Bay, Baja California, to Kodiak, Alaska (Welander, 1940; Claussen, 1959). Shad make no spawning runs south of San Francisco Bay because there are no streams of sufficient size. The Fraser River is thought to be the most northerly river in which they spawn (Carl, Clemens, and Lindsey, 1967).

Nothing concrete is known about the migrations of the shad in the Pacific Ocean but cir-

[4] U.S. Coast Guard Oceanographic Unit. 1969-1971. Monthly temperature charts, July 1969 to December 1971, available U.S. Coast Guard Oceanographic Unit, Airborne Radiation Thermometer Program, Bldg. 159-E Washington Navy Yard, Washington, D.C. 20390. [Processed.]

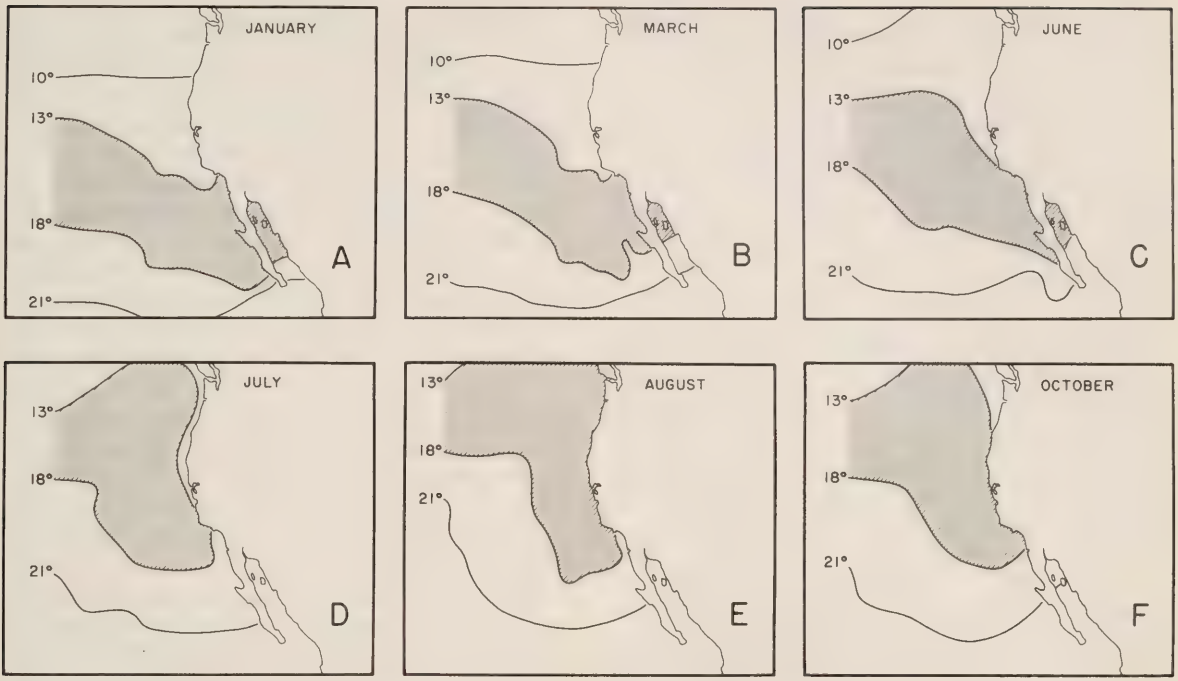

FIGURE 3.—Pacific Ocean average sea-surface temperatures and predicted shad distributions for selected months. (Temperature charts adapted from U.S. Navy Hydrographic Office, 1954.)

cumstantial evidence suggests a northward migration in summer and a southward one in winter as on the Atlantic coast.

If we assume that the migrations of shad in the Pacific follow the same specific ocean temperatures as do the migrations of Atlantic coast populations (an assumption that is supported by the similar relationships between peak movements into rivers and water temperatures on the two coasts), it is possible to make predictions concerning the Pacific migrations based on our knowledge of the distribution of 13° to 18°C waters along the Pacific coast.

During the months of December to April, the 13° to 18°C isotherms encompass an area extending from southern California to near the tip of Baja California (Figures 3A, 3B). We predict that the Pacific shad populations will be found to winter in this general area, a prediction strengthened by records of a few shad from San Pedro, Calif., in November and December (Smith, 1896). In May and June a general warming trend is noticeable along the coast, and the 13° to 18°C isotherms arch northward offshore (Figure 3C). Their northward movement is undoubtedly affected by the upwelling that occurs along the California and Oregon coasts and produces an inshore pool of cool water in spring and summer. We predict that the shad begin their northward movements at this time. If this be so, they are probably directed offshore in the area of this cool water. In July and August, 13° to 18°C waters occur over a wide range of the Pacific Ocean (Figures 3D, 3E). Shad might be located anywhere from Alaska (in some years) to Baja California. The reports, summarized by Welander (1940), of rare summer occurrences of shad at Kodiak, Alaska, and by Claussen (1959), off Baja California, are therefore not surprising. In September, cooling commences and results in a southward movement of suitable water and a contraction of its extent (Figure 3F). During this period we predict that the shad move southward with the 13°

to 18°C isotherms, resulting in their concentration off southern California and Baja California in late November and December and continuing at least until April.

The scope of regular migrations that we hypothesize as taking place on the Pacific coast (about 2,575 km, Columbia River to Cedros Island) is similar to that which is known to occur on the Atlantic coast (about 2,250 km, St. Johns River, Fla., to the Bay of Fundy).

DISCUSSION

Both the marine and freshwater migrations of shad appear to be regulated by water temperature. In the four rivers we have considered, the temperatures at which shad appeared in the river and at which peak movement occurred were remarkably consistent in spite of the great distances separating them. In all rivers except the St. Johns in Florida, water temperatures are increasing as the shad proceed upriver. Water temperature in this river is decreasing during the first half of the run, and the peak movement occurs at the lowest annual temperature. Nevertheless, the peak occurred in the same temperature range (15.5°-20.0°C) in the St. Johns as in the other rivers studied.

The precise correlation between temperature and the timing of the spawning migrations of the shad places the maximum number of adults on the spawning grounds when the temperature is optimum for the survival of eggs and young. In the Columbia and Connecticut Rivers, where our studies of shad movement were conducted at points close to the spawning grounds (Bonneville and Holyoke), peak migrations occurred at 18.0° and 19.5°C, respectively. Massmann (1952) working in the York River, Walburg (1960) in the St. Johns River, and Marcy (1969) in the Connecticut River have all reported the median spawning temperature, as shown by abundance of eggs, to be within the temperature range of 16° to 20°C. Leim (1924) and Bradford, Miller, and Buss (1964)[5] found that maximum hatch and survival of eggs and larvae occurred at 15.5° to 26.5°C. Temperatures below 15.5°C prolonged the time of hatching and reduced survival.

Since these optimum temperatures are reached later in the year at higher latitudes, the timing of the entry of shad into individual rivers must also be seasonally adjusted. Consequently, the earliest run occurs in Florida during the winter, and the latest runs in June and July in northern rivers such as the St. Lawrence and Columbia. This phase of the timing appears to be regulated by the adherence of shad to similar temperature regimes while at sea. As the ocean warms in the spring, the area occupied by water temperatures in the range 13° to 18°C moves gradually northward. By maintaining themselves in this thermal zone, shad arrive at the mouth of their home river when river temperatures are suitable for entry.

Of course, what we have described is a general migratory pattern of shad that is clearly associated with water temperatures both in the ocean and in the streams into which they run. Occasional shad are caught in the winter in Chesapeake Bay and in the Delaware and Hudson Rivers in the fall and winter (summarized by Walburg and Nichols, 1967, also recorded in our recoveries of Connecticut River shad shown in Figures 2A, 2F.) We learned recently that 14 shad were caught in a commercial trawl on February 10, 1972 at lat 41°16′N, long 71°39′W where the water temperature was 3.7°C at the surface and 4.1°C at the bottom. Nevertheless, as Walburg and Nichols stated: "The vast majority of fish, however, followed a regular migratory pattern." It may very well be that the observed temperatures associated with the presence of the majority of shad are preferred temperatures, not required ones, or they may be required only by a majority of fish. A small minority may be able to condition themselves to water outside the range tolerated by the majority. Experiments are needed to determine the upper and lower units of temperature tolerance of mature and immature shad, as well as their temperature preference.

It should be noted that we have related average ocean conditions to an average shad migra-

[5] Bradford, A. D., J. G. Miller, and K. Buss. 1964. Progress report summary on phase B-2 "to determine by bioassay techniques the inherent tolerance of shad during its egg and larval stages to specific environmental factors of the Susquehanna River and its tributaries. Pennsylvania Fish Commission, Benner Spring Fish Research Station, Bellefonte, Pa. (Unpubl. manuscr.)

tion. In particular years the ocean temperature regime may vary and change the usual locations of the shad. Moreover, we have related shad migrations to surface temperatures only. There is at present no information on the depths at which shad migrate. Walburg and Nichols (1967) recorded shad that were trawled at depths of 87 to 126 fm, and Leggett has similar records of recoveries of tagged shad at depths of 20 to 70 fm, again by trawl. These records do no more than provide estimates of the maximum depths at which shad migrate. These fish may have been captured near the surface as the trawl was being recovered.

On the basis of our observations on the behavior of shad in relation to temperature, we believe that the effect of a significant elevation of the temperature of a northern stream might be to initiate the shad run at an earlier date, provided that ocean temperatures are within the proper range. In a southern stream like the St. Johns River, Fla., where the run occurs during the natural cooling phase rather than the warming phase of the river, elevated temperatures could destroy the run of shad.

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AN EXPOSITION ON THE DEFINITION OF FISHING EFFORT[1]

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ABSTRACT

The term "fishing effort" is well defined in population dynamics literature. The term as defined in the population dynamics literature is, however, difficult to reconcile with broader definitions of fishing effort, particularly those having economic implications. The present paper discusses the distinction between the definitions and gives some examples in the context of allocating inputs, the capacities of fishing boats, and several stocks to the catch in a manner which maximizes profits. Managerial behavior is also an important input to the fishing process; this is discussed in a decision theory format where decision quality can be measured relative to entropy in the decision environment affording a comparison among decision environments in terms of information and an imputed valuation of a bit of information under various circumstances. The conventional measures of the quality of the decision environment are often based upon expected catch. Alternate measures are discussed which include the expected loss or the risk involved in the decision process.

The deployment of fishing effort is one of the fundamental components of fishery management. While fishing effort has been rather precisely defined in the population dynamics literature, effort has not been well defined in its broadest context. This paper considers the definition of fishing effort with special reference to the development of techniques which are useful not only for the definition of effort in the usual strategic sense, but for the definition of effort in the tactical and operational sense as well. This definition is requisite for considering fishing as a total system (see Rothschild, 1971).

The transformation of wild stocks of fish into the "catch" is generally considered to be mediated by the quantity of fishing effort expended in the process of harvesting the catch. The measurement of the magnitude of fishing effort is of central importance to the theory of the dynamics of exploited fish populations because the various "optimal" catches which are developed in this theory must ultimately be related to optimal quantities of fishing effort. On one hand it seems quite obvious that fishing effort should be related to quantities that can be thought of as "inputs" to the fishing process, quantities such as hours fished, fuel consumed, number of fishermen, etc. Therefore, it is at least to some extent somewhat paradoxical that the basic definition of fishing effort which is used in population dynamics, and commonly used in most fishery management applications, does not necessarily refer to any of these usual "inputs." Fishing effort is defined in terms of the catch; that is, one unit of real or nonnominal effort is simply the numerical fraction of the average population that is caught. In order to emphasize this point, consider two fishing fleets. Each fleet fishes on separate populations which are in every respect identical. The fleets make identical catches and, therefore, each removes identical fractions of the average populations from each population. By definition, then, these two fleets both exert the same amount of fishing effort. The fact that "inputs" are not implicit in the theory can be seen by identifying the first fleet as consisting of 100 modern trawlers and the second as, perhaps, 10 pleasure yachts that have been modified just enough to enable them to catch fish. Even though both fleets exert equivalent amounts of fishing effort, their inputs—indexed by, say,

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the costs of their operations—must differ considerably. This, of course, in no way invalidates the population dynamics theory and there are, in fact, methods for converting fishing effort, defined in terms of the magnitude of the catch, into numbers of fishing boats, etc. There is an extensive literature on this subject and, because of this, there is no need to prolong the discussion of this particular aspect of the fishing-effort problem. Rather, we shall concentrate on aspects of the problem of identifying and measuring inputs to the fishing process as well as discussing the methodology of relating the set of inputs to the outputs (the catch), which can, as we will see by the ensuing discussion, be treated in terms of several species and even, if necessary, in terms of strata (such as, for example, size classes) within several species. These aspects of the problem simply relate to the theory of production functions. Production functions have seldom been treated in fisheries, but when they have, they have been approached primarily from a regression analysis point of view. It is not clear, even given that we meet the assumptions of the estimation procedures and thus obtain credible statements on the "good properties" of the estimation procedure, that the curve fitting technique can do much more than describe, in an artificial way, the status quo; there is no inherently good advice in the curve fitting procedure on optimality; optimality must be implicitly assumed. What is needed are techniques of finding those combinations of inputs that produce extrema in the outputs, as well as to determine the sensitivity of this input-output system to changes in the magnitude of the inputs, and a reevaluation of the input-output system which will acknowledge the stochastic aspects of the decision process.

Our analysis of the fishing effort problem is divided into several parts. First, the fishing-effort problem is recast as a production function problem whereby valuable inputs to the fishing process are allocated among the outputs of the process in a manner which maximizes profit. In the particular example chosen the inputs are the capacities of three sizes of fishing boats in a fleet and the "catchable stocks" of two species of fish, yellowfin and skipjack tuna, whereas the outputs are the catches of the various species in the different boats. The components of the yellowfin and skipjack tuna catchable stocks are allocated among the various size vessels in the fleet to maximize profits. The technique used to explore the maximization of profits is linear programming. The technique enables the simultaneous exploration of fleet technological constraints, the interaction of multiple species as inputs to the decision process, and the range within which catches can be set without changing the nature of the profit maximization equation. Easy algebraic extensions of the model can be seen to have rather important implications. For example, instead of allocating two species of fish among three boat classes, the stocks of i species can be allocated among j classes of boats and k fishing nations. The ease of such an extension may, however, be somewhat deluding, particularly because of the difficulty in defining appropriate coefficients and constraints respecting the allocation among the k nations. Nevertheless the difficulty does not preclude solution and furthermore placing the problem in this context enables a much needed formulation of the problem of allocation of fish stocks among countries.

Most input-output analyses involve physical inputs and outputs. This was true in the example cited above. A classic example in fisheries is that of fishing power which is frequently related to fishing vessel horsepower. There are many instances, however, where the physical inputs (horsepower, fleet capacity, etc.) are less important than those related to the skill utilized by the fisherman in making managerial decisions such as where to fish, when to fish, when to stop fishing, etc. So, in the second part of this paper we consider the development of a decision theory model for adjudging fisherman skill in a "real world" probabilistic environment and show how the quality of the fisherman's skill in decision making relates to the entropy of his decision environment. Many important applications of this theory beyond the examples utilized in the text, such as the decision of whether to fish species a or species b when both species are available or whether to fish on one ground such as the eastern tropical Pacific tuna grounds or to move to an-

other ground such as the tuna grounds off the west coast of Africa.

The third part of the paper considers, given the possibility that inputs and outputs can be related and that decision skill can be judged, that different fishermen apply different criteria to the signals that they obtain from their decision environment. This question is discussed in terms of maximizing catch versus minimizing risk in attaining the catch. One of the main conclusions that can be derived from the following discussion is that advances toward the management of fisheries as a total system which considers the strategic, tactical, and operational hierarchies and the flow of information and material among these are not limited by analytic techniques. The limitation arises from a lack of explicit formulation of the kinds of data needed for the development of a total management system.

INPUT-OUTPUT ANALYSIS

Let us contrive a simple production function problem in a linear-programming context. This approach is treated in some detail by Dorfman, Samuelson, and Solow (1958). We should mention that the linear-programming technique is, of course, not without assumptions, and these are discussed in any operations research text (for another application of linear programming in salmon management see Rothschild and Balsiger, 1971). Violations of the assumptions required for the linear-programming model are usually handled by other techniques in mathematical programming theory, but these are, in general, computationally more difficult. In order to provide a semblance of realism to the problem, we use some now somewhat outdated data provided in Table 7 of Green and Broadhead (1965). We begin by assuming we have a fleet of 300-, 400-, and 500-ton seiners. The capacity of the fleet is calculated in Table 1.

The capacity for each size class of boat is an input in the production function. We also need to supply as inputs to the production function some raw material in the form of fish. Let us say that we are limited to 90,000 tons of yellowfin tuna and 120,000 tons of skipjack tuna. Then the objective of production is to maximize profits

TABLE 1.—The capacity in tons of a hypothetical tuna fleet in terms of various size classes of fishing boats.

Size of boat (tons)	Size of fleet (No. of vessels)	Capacity of each boat (tons)	Annual capacity of each boat (tons)	Total capacity for fleet (tons)
300	20	273	1,173	23,460
400	60	364	1,419	85,140
500	20	455	1,592	31,840

by maximizing the objective function: $Z = 8.65H_{11} + 7.32H_{12} + 10.66H_{21} + 9.01H_{22} + 7.75H_{31} + 6.53H_{32}$ where the H_{ij}'s correspond to the ith boat size ($i = 1, 2, 3$; where the integers refer to 300-, 400-, and 500-ton boats, respectively) and the jth species ($j = 1$ is yellowfin tuna and $j = 2$ is skipjack tuna). The coefficients in the objective function correspond to the weighted average profit per ton for the jth species caught by the ith boat as deduced from Green and Broadhead. Now with respect to the allocation of two scarce inputs—the capacity of various size vessels in the fleet and the catchable stock of the two species—to the production process, the capacity of the fleet generates the following set of constraint equations:

$H_{11} + H_{12} \leqslant 23{,}460$ tons (capacity of small boats)

$H_{21} + H_{22} \leqslant 85{,}140$ tons (capacity of medium boats)

$H_{31} + H_{32} \leqslant 31{,}840$ tons (capacity of large boats)

whereas the stock inputs (viz. the catch quotas) generate the following set of constraints:

$H_{11} + H_{21} + H_{31} \leqslant 90{,}000$ tons ("quota" of yellowfin tuna)

$H_{12} + H_{22} + H_{32} \leqslant 120{,}000$ tons ("quota" of skipjack tuna).

Because different size boats catch different proportions of yellowfin and skipjack, the ratio of these species in the catch of each size class of boat is essentially a function of the configuration of the boat and its equipment. We can thus consider the ratio of skipjack to yellowfin as a technological characteristic of the boat's size class and in order to maintain the character of the technology, we use the percentages of yellowfin in the catch as given by Green and Broadhead (300-ton boats, 57%; 400-ton boats, 48%; and

TABLE 2.—Optimal allocation of skipjack and yellowfin tuna in tons of fish to various size classes of fishing boats.

Species of tuna	Size class of boat			Total
	1 (300 ton)	2 (400 ton)	3 (500 ton)	
Skipjack	10,112	43,886	18,511	72,509
Yellowfin	13,347	41,253	13,328	67,928
Total	23,459	85,139	31,839	140,437

500-ton boats, 42%) to obtain the yellowfin:skipjack ratios of 1.32, 0.94, and 0.72, respectively, thus yielding the technological constraints:

$$H_{11} - 1.32H_{12} = 0$$
$$H_{21} - 0.94H_{22} = 0$$
$$H_{31} - 0.72H_{32} = 0$$

Table 2 gives the maximization of the objective function which yielded $1,248,835 in tons of fish. The optimal solution then indicates that in the process of production, the entire capacity of the vessels was utilized. Because the catchable portion of the stocks was greater than this capacity, 22,070 tons of yellowfin and 47,489 tons of skipjack were unused by the fishery (slack variables). Note also that the catch of skipjack is greater than that of the more valuable species, yellowfin, because of the technological constraints enforcing the lower yellowfin:skipjack ratios in the more numerous larger boats. The imputed marginal values, the so-called shadow prices of a ton of yellowfin and skipjack are, of course, zero because the capacity of the stock to produce these quantities of fish was not reached; but, however, the capacity of the vessels was reached and, therefore, the marginal value of an extra ton capacity on the 300-, 400-, and 500-ton boats is imputed to be $8.08, $9.81, and $7.04, respectively. These shadow prices are simply the weighted average profits for each size class, e.g.:

$$\$8.08 = \frac{10,112}{23,459}\,7.32 + \frac{13,347}{23,459}\,8.65$$

Perhaps of even greater interest is the way in which the various production inputs interact with one another. For example, in this particular problem, we could increase the yellowfin and skipjack catchable population constraints *ad infinitum* without changing the nature of the optimal solution. But if we were to reduce the catchable population of yellowfin tuna from 90,000 tons to 67,930 tons or skipjack from 120,000 tons to 72,510 tons, we would eliminate the yellowfin and skipjack slack variables, respectively, and these would no longer be in the optimal solution. Putting it another way, insofar as this particular problem is concerned, the nature of the solution, in terms of, for example, those variables to which some monetary value greater than 0 would be imputed, would not change until the catchable population of yellowfin dropped below 67,929 tons or skipjack to below 72,510 tons. The point of this is that (again insofar as this particular problem is concerned) we are not going to change the nature of our optimal solution for any catchable populations of yellowfin >67,929 tons or of skipjack >72,510 tons. This means that it may not be necessary to be concerned with precise estimates of the catchable population if the catchable population is, as in this case, much larger than the lower bounds for changing the solution. This reflects, within the scope of the model, the bounds within which changes in the catchable population will have no effects upon the components of the objective function. This demonstrates, in an analytical way, that population dynamics theory may offer solutions that are, in some instances, apparently more precise than that which is needed. In other words, we frequently postpone resource decisions to obtain a certitude in our estimate, which would not change the optimal solution of the input-output process. This postponement is almost never without social costs which may be substantial.

Now with respect to modifying the fleet capacity, we can, given the stock constraints, increase the capacity of the small boats to 62,250 tons or decrease it to 0 tons. If we exceed the upper bound then this means that we need to catch at least 38,790 additional tons of fish and, of these, 57% must be yellowfin amounting to an additional catch of 22,110 tons of yellowfin. But if we catch this additional quantity of yellowfin, we will use up our 90,000 tons of yellowfin, dropping the yellowfin slack variable from our solution. At the lower bound, it is obvious that if we constrain the catch of small boats to be 0,

we eliminate the variables corresponding to the catch of small boats from our optimal solution. The interpretations of the sensitivity of the 85,140-ton constraint upon the maximum catch of the 400-ton boats and the 31,840-ton constraint upon the maximum catch of the 500-ton boats are identical.

It is perhaps more subtle that the *full* utilization of the excess yellowfin tuna capacity is impossible because the 85,140 tons of fish that would be caught by the 400-ton boats consists of $85{,}140 \times 0.48 = 40{,}867$ tons of yellowfin tuna (the 0.48 is the appropriate technological constraint). To use up the yellowfin tuna surplus we would need to catch roughly an additional 50,000 tons of yellowfin tuna, but if we did this we would need, by virtue of our technological constraint, to catch a total of 90,000 $(0.48)^{-1}$ tons of fish which clearly exceeds the fleet capacity. With respect to the technological constraints, we could in the 300-ton boats, for example, increase the right-hand side of the equality to 23,460, which would modify the solution by eliminating any catch of skipjack by the small boats (in other words, H_{12} would be eliminated from the optimal solution). On the other hand, we could reduce the equality to —30,967, and if we did this, the catch of yellowfin by small boats would be eliminated from the solution $[(30{,}967)(1.32)^{-1}] = 23{,}460$. The negative right-hand constraint reflects more upon the nature of the solution than reflecting any physical meaning.

It is clear that since we used all the capacity of our hypothetical fleet that any increase in profits will not induce us to catch more fish. On the other hand, by inducing a negative profit we can show that in these instances some of the boat-species combinations should not be filled to capacity (Table 3). Thus we would have to lose

TABLE 3.—The lower bound of profit and "sensitivity" for yellowfin and skipjack tuna caught by various size classes of fishing boats. The results are reported in dollars.

Species of tuna	Boat class	Profit per ton in problem	Lower bound of profit	"Sensitivity"
Yellowfin	1	8.65	—5.54	14.19
	2	10.66	—9.58	20.24
	3	7.75	—9.07	16.82
Skipjack	1	7.32	—11.41	18.73
	2	9.01	—10.02	19.03
	3	6.53	—5.58	12.01

$5.54 per ton of yellowfin to generate empty capacity space in class 1 vessels. The difference between the lower bound profit and the profit used in the problem is a measure of sensitivity. We note for example that the behavior of the fleet is most sensitive in class 3 boats where a $12.00 decline in profits would generate excess fleet capacity, or a $16.82 decline in yellowfin profit would also generate excess fleet capacity.

Now let us make an apparently slight but important modification in our problem. We will keep everything the same, but we will increase the capacity of the small boats from 23,460 tons to 65,000 tons. In the first example we were interested, primarily, in the sensitivities of our model to changes in the constraints. Now, however, it is of interest to compare the optimal solutions in the two examples (Table 4). Thus by adding an extra 42,000 tons of capacity to the small boats, we increase the skipjack catch by only 16,000 tons and the yellowfin catch by 22,000 tons. We have not, owing to the constraints, caught an additional 42,000 tons of fish. We have caught proportionately more yellowfin than skipjack, increasing the optimal solution from $1,248,835 to $1,562,133. In the second example, in contrast to the first, we have used

TABLE 4.—A comparison of optimal solutions in Example I where the capacity of the small boats is 23,460 tons and in Example II where the capacity of the small boats is 65,000 tons. The comparison shows the optimal allocation in tons of fish for each example.

	Example I				Example II			
	Boat class				Boat class			
Species	1	2	3	Total	1	2	3	Total
Skipjack	10,112	43,886	18,511	72,509	26,831	43,886	18,511	89,228
Yellowfin	13,347	41,253	13,328	67,928	35,418	41,253	13,328	89,999
Totals	23,459	85,139	31,839	140,437	62,249	85,139	31,839	179,227

up our yellowfin tuna resource and have reduced the unused portion of the skipjack resource from 47,489 to 30,769 tons. In addition, we have 2,749 tons of empty capacity in the small boats. This excess capacity is enforced, to a large extent, by the technological constraints, and we can see that these modifications would enable utilization of the empty space with skipjack tuna. Thus we can formulate, in a programming context, the relation between the inputs and outputs of the fishing process. If we agree that the management process requires the kinds of information that are required in the programming problem, then we can see that we have been collecting the wrong kinds of information on our fisheries.

To sum up, then, we have discussed the production function from a linear-programming point of view. We have picked two possible examples out of an infinitude of possible examples. The particular examples we have chosen may be criticized from the point of view of their immediate applicability to real situations. This criticism is correct and indeed it is quite an important criticism which simply reflects that in these tuna fisheries and most of the other fisheries in the world, we simply neither have nor collect the kinds of data that we need to enter into an analytic evaluation of what is perhaps the most critical of fishery management problems, the allocation of fishery resources among various user groups throughout the time stream. This is not because these data do not exist; it is because, in general, explicit attempts have not been made to gather these sorts of data. It is a contradiction to deny the usefulness of utilizing the physical metric for managing fisheries and to not provide mechanisms for obtaining the kinds of data that are required to manage the fisheries in the appropriate way, in the value metric.

The point, then, of demonstrating the linear-programming technique is to (1) call attention to a powerful allocation tool which can be used for guidance in, for example, a serious contemporary tuna problem, the allocation of the tuna catch among the nations; (2) highlight the important difference between the inputs of the fishing process and the fishing effort used in population dynamics; (3) point out the nature of sensitivity in a programming context which can show, for example, that when we examine the entire productive process that, given the right kinds of economic data, we can think of managing stocks in terms of, say, an upper and lower bound on catch which could free research effort, for example, to other productive endeavors; and (4) finally, because of recent confusion on the subject, suggest that the term fishing effort be utilized only in the context in which it is defined in the population dynamics literature and that the term fishing inputs be reserved for the more general connotation of "fishing effort."

INTERPRETATION OF FISHING SKILL

Now let us look at the input process in a little more detail. When we do this we have to admit that we can, having established the definitions of fishing effort and fishing inputs, especially if we restrict our consideration of management to manipulating physical quantities of the catch, relate at least some but, in general, not all of the fishing inputs to fishing effort through the appropriate catchability coefficient. This enables the dynamicist to have comparable measures of the abundance of fish from time-space point to time-space point. Again the adjustment of estimates of abundance to common units through the computation of fishing power is well treated in the literature, and we will not belabor it here, except to note that fishing power is almost always calculated on the basis of some usually single physical feature of the fishing vessel such as engine horsepower, etc., or simply on empirical differences in the catch-per-nominal-effort that is obtained by the fleet. Differences in fishing power are certainly more complicated than comparisons among the physical attributes of the fishing vessels would indicate. A considerable portion of the variability in fishing power among fishing units can be attributed to variability in the skill of the fishing skipper. This assertion is subsumed in Figure 1.

Figure 1 is hypothetical and shows that the quality of fishing skippers could be a more important determinant of the "quality" of a fishing operation than the physical characteristics of the boats. We might guess that boats that are phy-

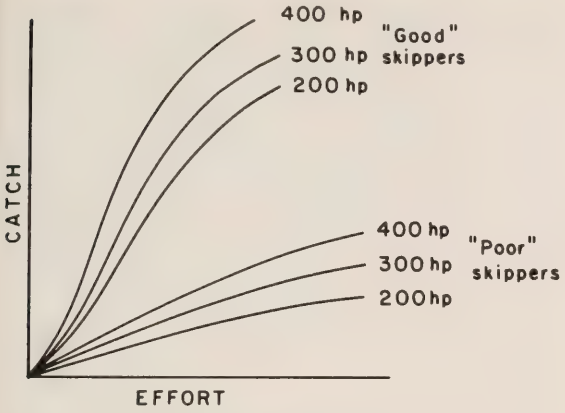

FIGURE 1.—Hypothetical relation between catch and effort for boats of varying horsepower and for "good" and "poor" skippers.

sically different in some important index in a ratio of say 2:1 may exhibit a range in catch-per-input where the best boat is, say, 10 or more times better than the poorest boat. The greater effectiveness of some boats over other boats can in large part be attributed to the skill of the skipper. This is ignored in many analyses primarily because this question of skill has never been appropriately formulated. In this section, we begin to develop some examples which contribute to the rudiments of analysis of the behavior of the skipper as an input to the production function—in terms of how a skipper perceives the fishing environment—and then mention the problem of the utility that the skipper places on the various signals that he obtains from the environment. We make a point of stressing that the relation of the input vector to the output vector in the fishing process is usually considered to be deterministic by students of the fishing process. Another approach is to use an average vector for inputs and assume an average vector for outputs. Unfortunately, it is unlikely that fishermen perceive the decision environment as either deterministic or average and we make use of this observation in our additional considerations.

In order to demonstrate these points we will construct a branch of a very simple decision tree which can serve as a framework for future analysis. The branch of the tree is shown in Figure 2. This is the skipper's decision environment. Nature deals the skipper good fishing, Θ_1 or poor fishing, Θ_2. The skipper has an opportunity to take a glimpse at the environment. This interpretation of the glimpse is denoted by $P(\hat{\Theta}_i | \Theta_j)$ where $\hat{\Theta}_i$ is his guess of Θ_i ($_j$ does not necessarily have to equal $_i$). If the skipper guesses $\hat{\Theta}_1$, then he commits himself to a fishing operation, but if he guesses $\hat{\Theta}_2$, he moves to a less risky area and fishes. In this less risky area, nature deals new fishing conditions Θ_1' and Θ_2'. The reward for any particular fishing action is specified in Figure 2. We wish to use this model to show how chance enters the decision process.

We set

$$P(\Theta_1) = 0.2$$
$$P(\Theta_2) = 0.8$$
$$P(\Theta_1') = 0.8$$
$$P(\Theta_2') = 0.2$$

and examine three conditions:

Condition I

The skipper is perfectly skilled and thus $P(\hat{\Theta}_1 | \Theta_1) = P(\hat{\Theta}_2 | \Theta_2) = 1$ and $P(\hat{\Theta}_1 | \Theta_2) = P(\hat{\Theta}_2 | \Theta_1) = 0$. The expected value of the branch

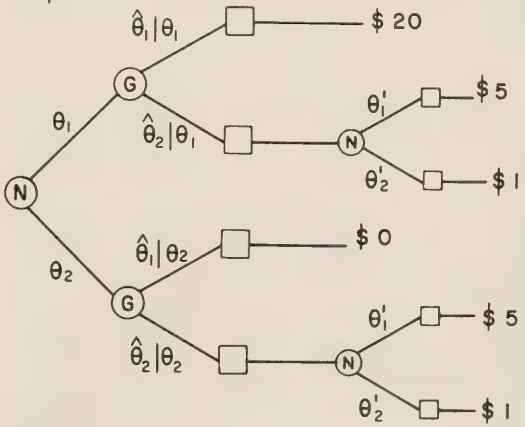

FIGURE 2.—Branch of decision tree showing various events and payoffs. (For a discussion of decision analysis see Raiffa, 1968.)

is \$7.36 with a measure of entropy of 130 centibits. (Entropy is defined in the usual way, but measured in centibits rather than in bits owing to the relatively low degree of "randomness" in these hypothetical examples.)

Condition II

The skipper is quite skilled and thus $P(\hat{\Theta}_1 \mid \Theta_1) = 0.9$, $P(\hat{\Theta}_2 \mid \Theta_1) = 0.1$, $P(\hat{\Theta}_2 \mid \Theta_2) = 0.9$, $P(\hat{\Theta}_1 \mid \Theta_2) = 0.1$ (say). The expected value of the branch under this condition is \$6.71, and a measure of its entropy is 172 centibits.

Condition III

The skipper is unskilled and thus $P(\hat{\Theta}_i \mid \Theta_j) = 0.5$ for $i = 1,2$ and $j = 1,2$. The expected value of the branch under this condition is \$4.10, and a measure of its entropy is 209 centibits.

It is important to observe, in respect to the first example, that if nature dealt the Θ_i's with probability of 1 or 0 then entropy would be 0. Nature has not, in our example, chosen to deal the Θ's deterministically and, therefore, 130 centibits is the lower threshold of entropy, given that probabilistic behavior of nature remains the same.

Now, we note several interesting features of this analysis which are capable of many simple extensions. First, we have distinguished between the contribution to entropy made by the behavior of nature and the behavior of the fishermen. Second, we have quantified the randomness in the decision problem by measuring the randomness in bits and thus have the opportunity to quantify the required skill of the skipper; because when nature deals a low-entropy probability structure, relatively less skill is required to achieve equivalent results. Third, we can valuate the skipper's decision process as an input to the production function. For example, under Condition III an unskilled skipper can produce, on the average, \$4.10 worth of fish in a 209-centibit environment, but a quite skilled skipper [skill being measured by $P(\Theta_i \mid \Theta_j)$] can *by his skill* reduce the entropy 37 centibits. The 37 centibits being a difference between entropies is thus a measure of information, and in this example 37 centibits of information are worth \$2.61 or roughly 7 cents per centibit. A perfectly skilled skipper reduces entropy an additional 42 centibits, the additional information yielding 65 additional cents, or about 1.5 cents per centibit. In other words, in this example, the information accrued in moving from unskilled to quite skilled is about the same as that accrued in moving from quite skilled to perfectly skilled, but the value of a unit of information is 4 times greater in moving from unskilled to quite skilled than a unit of information acquired when moving from quite skilled to perfectly skilled.

DECISION CRITERIA

Thus, we have considered a model of the way in which the skipper "processes" signals from the fishing environment where the quality of his processing ability is measured relative to nature-generated entropy in the decision environment. We must now consider how the skipper valuates the signal and the criteria that he places upon these signals. First, consider what might be a traditional approach of where to fish. In this approach we have a field of expected catches and upon examining this field we advise the skipper to fish at the location where the expected catch is highest. A second approach is to examine the field of space-time points and consider the distribution of catches at each space-time point. Let us consider a simple aspect of this problem; two space-time points A and B, at which the fisherman's perception of the catch is that it has an approximately normal distribution. Figure 3 shows these two distributions. The figure also indicates the point on each distribution below which the fishing operation will lose money. If we look at only the expected catch, we would advise fishing at A. But if we examine the risk (that is, $\int xf(x)\,dx$, evaluated from $-\infty$ to the break-even point) we note that fishing at B will minimize risk, and if this were our criterion we would fish at B. We should note further that the fish-

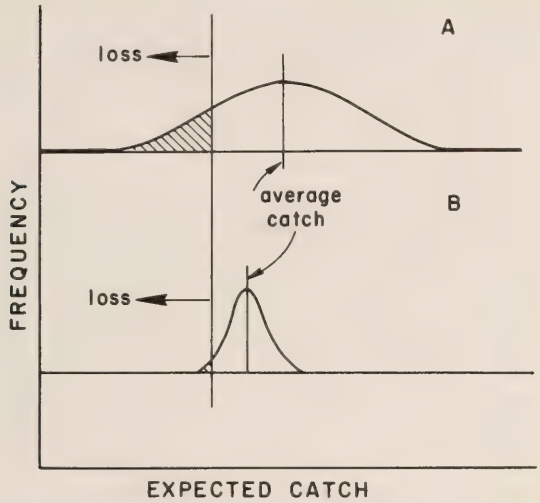

FIGURE 3.—The distribution of catch at two locations showing the average catch and the loss region.

erman samples the distribution dealt by nature and his sample can be biased and vary in precision. His perception of the correct action depends upon his view of how many times he can sample these distributions. This is clear because if the fisherman has only one chance to go fishing, he should choose B to minimize his risk, but if he has many chances to go fishing, he should choose A to maximize his gain since the sampling risk will be decreasing inversely proportional to the square root of the number of chances that the fisherman has.

A reasonable criterion for choosing a fishing location might be the expected gain less the expected loss; e.g.,

$$\int_a^b xf(x)\,dx - \int_a^B xf(x)\,dx$$

where $f(x)$ is the distribution function of the fisheries earnings, a is the minimum value of this function, b is the maximum value, and B is the break-even point. Note that this general form can be written in several alternative ways. But even the establishment of such a criterion is not sufficient to measure the skipper's behavior. We need to know the utility that the skipper places in any value of the criterion.

ACKNOWLEDGMENTS

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ADDENDUM

The reader interested in applications of decision theory should examine "Marine decisions under uncertainty," by John W. Devanney III, Cornell Maritime Press, 1971, which was discovered while the present paper was in proof.

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UNDERGRADUATE EDUCATION OF FISHERY SCIENTISTS[1]

WILLIAM F. ROYCE[2]

The requisite preparation and training for the profession of fishery scientist[3] has received much attention from faculties giving instruction related to fishery problems and from a number of people who have examined the educational problem in some depth, notably Deason (1941), McHugh (1968), Paulik (1968), and Carlander (1970). Almost everyone has been dissatisfied with the curricula available. Those of us who are concerned are well advised to ask what we can do to improve our preparation of fishery scientists for their roles in society as scientists and as citizens.

The traditional approach to fishery science was through training in natural history, especially in ichthyology and limnology. The first special courses in fisheries in North America were developed in aquaculture and fishing. Later, courses were offered in the biology and ecology of fishes and in fishery management. It was recognized generally, however, that most of the training of fishery scientists should be in biology and a degree in fisheries was equated with a degree in either biology or zoology by many agencies that employed fishery scientists.

The traditional approach is now being challenged from many directions. The problems of public fishery management are only part of the immensely complex problems of environmental management, the solution of which involves predominantly the management of people. The proliferation of specialized courses in biology causes many fishery students to wonder whether most of them are useful. The diversity of fishery jobs stimulates others to inquire what set of courses should be taken for each. It is now accepted generally that an undergraduate biology major is not the best preparation for most fishery jobs, and the basic question is asked—What is the best education for each kind of fishery job?

ROLE OF FISHERY SCIENTISTS

The common division of fishery science into management and research fails completely to indicate the diversity of jobs that are filled by fishery scientists. Carlander (1959) in his survey of technical fishery careers used the categories: (1) fish culture; (2) management; (3) survey and trouble shooting; (4) research; (5) education; and (6) administration. Later (1970) he listed a sampling of fishery courses and included a number of additional subjects that might well be job categories: (1) pond and lake management; (2) hatchery management; (3) fishery technology and economics; (4) pollution biology; and (5) population dynamics. Obviously, the category of fishery technology can be separated into commercial fishing and fish processing technology and the category of fish culture can be extended to include shellfish culture.

A much more diverse group of categories is included in Hall's (1969) review of fishery occupations on an international basis. He considers that most of the personnel engaged in the following fishery activities require a high degree of special fishery knowledge: (1) seagoing and other personnel in the primary sector; (2) processing, distribution, and marketing personnel; (3) management, government administration, enforcement and development personnel; (4) research and education personnel; and (5) economists and statisticians. In addition he lists

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[3] Included in this category are all fishery resource workers who normally are required to have a baccalaureate degree or higher for the job they hold.

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ancillary industries associated with the construction of gear, vessels, processing equipment, and harbors and reservoirs that require personnel with an awareness of fishery problems. Obviously, only part of the occupations in both lists requires a science degree—the topic of this discussion.

Further, an examination of the publications of any major fishery agency reveals many diverse research topics, each of which could be discussed adequately by an individual only after years of specialized experience in graduate school or on the job. For example, recent issues of the *Journal* and *Bulletin* of the Fisheries Research Board of Canada include lengthy articles in each of the following areas of study: (1) biochemistry of pesticides, heavy metals, etc.; (2) fish and invertebrate physiology; (3) animal behavior; (4) ecology; (5) population dynamics; (6) life histories of animals of many phyla; (7) ichthyology; (8) genetics; (9) hydraulic engineering; (10) marine biology; (11) limnology; (12) oceanography; (13) microbiology; (14) pathology; (15) mathematics; (16) resource economics; and (17) fishery business administration.

This list could be expanded considerably but with little reinforcement of the conclusion that specialists on many topics contribute to fishery knowledge and aid in fishery decisions. Obviously, many problems must be studied by teams of experts who can apply their individual skills to a problem in which they share a common interest and concern.

Still further evidence of diversity may be found among employers of fishery scientists. Government fishery agencies are the principal employers, but nonfishery agencies and industry appear to be offering more and more jobs. Outdoor recreation agencies; water control and water quality agencies; soil, range, and forest resource agencies; and industries that use water are finding increasingly that they have enough fishery problems to warrant hiring fishery scientists. In addition, the fishery agencies are finding that the management of the fishery resources requires that they participate frequently in decisions about the use of water and land. It is apparent that many fishery scientists need at least to be aware of if not expert in the problems of using other natural resources.

THE CHOICE OF BACCALAUREATE DEGREE, MASTER, OR DOCTORATE

Soon after an aspiring fishery scientist has embarked on his education he faces a decision about when to stop and seek a job. He will probably be advised to seek graduate work if his scholarship is adequate and if he can finance it. If he does he will be a part of the one-fifth of the biologists who have recently sought advanced degrees (Terman, 1971). The brilliant student can get a fellowship or assistantship, so his decision may depend on whether he wants to spend the extra time; but to other students graduate work may require a major sacrifice. Will the added breadth of knowledge or specialization be worth the time and cost?

The roles of fishery scientists are not clearly separable according to terminal degree attained by them, but most of those with a baccalaureate are in fishery management and most of those with a doctorate are in teaching or research (Table 1). Many of those with a baccalaureate, however, are engaged in research or administration. Those with a master are engaged extensively in research, management, and administration; but a larger proportion of them than of the other two groups are in research and administration.

The divisions among fishery research, management, and administration are blurred, however, in other ways. All three require an ability to investigate problems but research will probably involve the solution of sophisticated scientific problems; management, a mixture of scientific, technical, and social problems; and administration, a mixture of social, economic, and political problems. All three require an understanding of the general environmental problems of our society, but these will probably be of greatest concern in administration. All three require an ability to communicate, but with different audiences. Additional blurring occurs because most fishery scientists divide their time among research, administration, and management or teaching.

TABLE 1.—Breakdown of respondents from Pacific Fishery Biologists by types of professional activities and fishery, highest degree attained, major subject, employer, and institution of origin.[1]

Item	Duties ≥40%[2]					Type of fishery ≥60%[3]	
	Fishery research	Fishery management	Teaching	Administration	Others	Recreational	Commercial
N 324	116	100	19	95	33	117	134
Highest degree							
B.S. 183	60	74	0	26	10	73	76
M.S. 85	33	22	1	32	11	34	36
Ph.D. 54	23	3	18	16	3	9	22
Years since last degree							
<10 126	57	47	10	19	17	53	46
10-29 115	38	35	5	36	10	40	52
>19 79	18	17	3	40	6	22	36
Major subject							
Fisheries 225	82	72	12	64	22	84	98
Biology, zoology 73	27	22	6	22	6	27	26
Employer							
NMFS 48	33	4	0	13	2	1	42
BSFW 24	5	3	3	8	7	11	4
State fisheries 154	46	78	0	41	9	79	49
Nonfisheries 30	2	8	1	14	9	13	4
Canada fisheries 14	4	5	0	7	1	4	8
Universities 32	13	0	15	7	2	4	14
Industry 7	4	2	0	1	2	3	1
Institution							
Univ. Washington 81	38	21	6	26	1	14	54
Oregon State Univ. 65	12	33	2	19	10	33	18
Other large univ. 73	27	21	3	22	5	30	29
Two or more univ. 63	23	12	7	23	10	23	19

[1] Nonresponses and certain minor categories have been omitted.
[2] The respondents who indicated a division of duties of 60-40 or 50-50 are included in two categories.
[3] The respondents who indicated a division between the two fisheries of 50-50 have been omitted.

Another separation of functions is between investigative and decision making activities. It may be assumed that research is predominantly investigative, administration is predominantly decision making, and management is both investigative and decision making.

In actual practice it appears that a majority of the fishery scientists in western North America have no more than a baccalaureate and are engaged in fishery management and administration. The responses (324) to a recent questionnaire to members of Pacific Fishery Biologists (PFB) indicated that 56% had only a baccalaureate degree, 26% had added only a master, and 17% had a doctorate. When queried about their activities 36% of the respondents said they were engaged in fishery research for 40% or more of their time, 31% in fishery management, 29% in fishery administration, 6% in teaching, and 10% in other activities, most of which were water management. (Some said they were engaged for 40% or more of their time in each of two activities and hence were counted twice in the above breakdown.)

It should be noted that the overall projections of supply vs. demand for Ph.D.'s indicate an oversupply for the needs of basic research and teaching and an expectation by many of a search for employment elsewhere (Cartter, 1971; Terman, 1971). The natural resource agencies and offices should expect an influx of Ph.D.'s trained in other areas during the 1970's.

The role of a person with a terminal master degree appears to be primarily in research and administration. A higher proportion of the members of PFB with a master degree than of those with either a baccalaureate or doctorate were engaged in administration, and the proportion of them that were engaged in research was nearly as high as the proportion of those with a doctorate so engaged. The master's training provides either the breadth of education that gives a person a wide choice of jobs or a special education for a particular job. It appears to be

especially useful to the person who works after earning a baccalaureate and then decides to obtain more education for clearly defined reasons.

Thus, the demand for fishery scientists will probably remain, as it has been, predominantly for baccalaureates; and this demand will coincide with the inclination of a majority of students to earn no more than the baccalaureate. The implications for the fishery educator seem clear —prepare an undergraduate student for a job if he intends to terminate his formal schooling with a baccalaureate and prepare him for graduate work if he plans immediately to work for an advanced degree. "Preparing a student for a job" does not mean training him extensively in techniques that he could learn as well or better on the job; rather it means preparing him as a scientist and citizen so that he can choose among a reasonable number of job alternatives and progress rapidly in the job that he finds.

SURVEY OF OPINION REGARDING FISHERY CURRICULA

Opinions and criticism of fishery curricula are frequently expressed by two groups of people, both of which should be regarded as biased: fishery faculty and employers. Fishery faculty tend to be oriented toward basic research and the necessity for doctorate degrees, which most of them have. They may even suggest that persons who get only a baccalaureate degree are likely to be only research technicians. Employers are necessarily concerned with the immediate problems of getting a job done and having employees who can do the job well with a minimum of added training. They are usually less interested in the capability of a new employee to grow in skill and take over major responsibility at a later date. Consequently, it was deemed useful to obtain opinions from others.

During the spring of 1971 it was possible to sample the opinions of members of the PFB with respect to fishery curricula. Membership in the organization, according to the bylaws, is "limited to graduates of universities of recognized standing who possess a degree in the biological sciences who are professionally engaged in fishery biological research and who have completed at least one year's cumulative service in research with some organization following graduation provided that employment in an organization in one of the following areas shall be necessary for membership: Alaska, British Columbia, Washington, Oregon, California, Idaho, and Hawaii." The organization included 751 active members in May 1970, a considerable fraction of the estimated 5,500 fishery biologists who were employed in the United States on July 1, 1970 (Martin, 1971).[4] The members were affiliated with one provincial and six state departments of fisheries or fish and game, two Federal fishery agencies, three Canadian fishery agencies, nine nonfishery government agencies, seven nonfishery industries with environmental problems, twelve colleges and universities, and the California Academy of Sciences (Table 1). Either notably absent or scantily represented were fishery scientists employed either in aquaculture or in the fishing industry. Probably underrepresented were fishery management biologists because of the requirement by PFB for professional engagement in fishery research. Subject to these qualifications the organization probably represented quite fairly at the time the fishery scientists in the western United States. Also canvassed were persons on the mailing list for the Northwest Fish Culturists Conference and student groups at the University of Washington.

The opinions about most useful and least useful subjects required somewhat arbitrary and subjective classification of the subjects into not more than 10 groups, as follows:

0) Function and methods
1) Biological sciences
2) Chemistry, physics, and mathematics
3) Natural resource sciences and management
4) Social sciences
5) Engineering and technology
6) Administration
7) Humanities and liberal arts
8) Communications
9) Other fields

[4] Martin, R. G. 1971. Potential employment market. *In* Items for fishery scientists from the Sport Fishing Institute. Jan.-Feb. 1971.

In the interest of saving space, no more than five subjects were coded for any one reply. When two or more subjects listed under the same code number were named, that code number was listed two or more times. When the answer was "all biology courses," however, the biology code number was listed once.

Further comments were classified in groups under the following general headings:

0) Miscellaneous comments or no comment
1) Increase practice and experience
2) Improve quality of courses
3) Improve curriculum
4) Help select and understand jobs
5) Arrange continuing education

COMPARATIVE USEFULNESS OF SUBJECTS

After the data had been coded, they were sorted and listed by the computer. The number of times that each subject was mentioned by respondents in each category was determined, and the total was computed as a percentage of the number of respondents.

The percentage of respondents that mentioned a subject as most useful, as least useful, or one that the respondent wished he had added to his college courses or taken in greater depth is regarded as an index of the usefulness of the subject. Inclusion in the most useful or the least useful category depended on inclusion of the subject in the respondent's training. The subjects of average usefulness were not mentioned, and there is no way of considering such a status from the data. The last class of subjects, subjects that the respondent wished he had added or taken in greater depth, is, of course, not limited to subjects taken in the university; but presumably many respondents would think first of subjects that they had taken but not as completely as they might have.

One of the difficulties in evaluating answers was the distinction between a general course, for example, in biology, and a collection of advanced courses that might also be called by the same name, in the example given, biology. Some respondents made this distinction clear; others did not, especially some who had taken their college work many years ago.

The outstanding characteristic of the responses is the inclusion of almost every subject among someone's most useful subjects and someone else's least useful subjects. It appears that subjects considered by most people to be very useful were ranked as the least useful by a few people who had special difficulties with a course, such as a quarrel with the instructor or a bad grade. Accordingly, it is felt that a designation of a subject as least useful by 1 or 2% of the respondents is not of particular significance unless the course was one that relatively few respondents would be expected to take.

The rating of subject groups is shown in Table 2. The groups are ranked starting with the one that was considered to be most useful by the greatest percentage of respondents and ending with the one that was considered to be least useful by the greatest percentage of respondents. Only the top twelve in any category have been ranked. The results are discussed in the following paragraphs.

The ranking of English-scientific writing as the most useful group of subjects may surprise many scientists, especially the younger ones who are preoccupied with learning science, but undoubtedly it reflects the broad experience of the applied scientists, who have repeatedly faced the need to communicate their findings. Only a few respondents rated these subjects as the least useful, and some of these specified that they objected to English literature or creative writing courses.

Public speaking, another method of communication, ranked eleventh among the subjects listed as the most useful and fifth among the subjects that should have been added or taken in greater depth. Those rankings probably reflect the failure of many fishery scientists to take public speaking and their general need for it later.

Communication in a foreign language was at the other end of the scale, however, first among the courses rated as least useful. Such courses are apparently a waste of time for most students but are needed by a few.

The next surprise for those who consider fisheries as essentially biology is the second place

TABLE 2.—Percent of responses naming undergraduate subjects as most useful, least useful, or one that should have been added or taken in greater depth.

Subject group	Most useful		Least useful		Should have been added or taken in greater depth	
	% of respondents	Rank	% of respondents	Rank	% of respondents	Rank
English, scientific writing	44	1	3	--	21	2
Biostatistics, population dynamics, computer use	34	2	2	--	44	1
Zoology	30	3	2	--	1	--
Fisheries, fishery biology	27	4	1	--	5	12
Mathematics, calculus	27	5	4	11	20	3
Chemistry, inorganic	23	6	12	4	5	--
Oceanography, limnology, pollution study	16	7	0	--	12	4
Ecology	16	8	0	--	8	10
Ichthyology, systematics	16	9	3	--	2	--
Physiology, cytology, embryology, morphology, etc.	13	10	6	8	9	9
Public speaking	10	11	1	--	12	5
Fishery management	10	12	1	--	4	--
Aquacultural sciences	8	--	4	12	7	11
Economics	4	--	4	--	12	6
Administration	0	--	1	--	12	7
Physics	6	--	5	10	2	--
Agriculture	0	--	5	9	0	--
Chemistry, organic	2	--	6	7	5	--
Advanced biology	2	--	6	6	3	--
Botany	7	--	7	5	4	--
Social sciences (except economics)	1	--	14	3	10	8
Humanities, liberal arts	3	--	16	2	4	--
Foreign language	2	--	21	1	2	--

ranking of biostatistics-population dynamics-computer use and the fifth place rating of mathematics-calculus. Both of these subject groups ranked even higher among those that the respondents wished they had added or taken in greater depth.

Biology, botany, and zoology courses varied greatly in their usefulness. General zoology ranked third among those listed as the most useful, ichthyology and systematic zoology ranked ninth, and a group of advanced zoology courses ranked tenth, largely because of the inclusion of the physiology of resource animals. Other advanced zoology courses and botany were more frequently among those listed as the least useful than among the most. Many respondents noted these as "too specialized" or "memory type" courses that they objected to. On the other hand, a few people rated them most useful.

Chemistry courses were viewed much like biology courses. The general courses were ranked relatively useful, but the advanced courses were rated not useful by more respondents than those who considered them useful.

The natural resource sciences also varied greatly in their usefulness. Fisheries and fish biology courses ranked fourth among those listed as most useful and fishery management twelfth. Aquacultural science, including pathology, parasitology, nutrition, and genetics as applied to fishery resource animals, varied greatly in usefulness (sample population was underrepresented in aquaculture). Apparently these are specialized courses, needed only by a few people. Other natural resource sciences, such as wildlife science or management, forestry, soil science, and land management, also varied in their usefulness.

The opinions about the usefulness of the social sciences were anomalous. Almost all of the social sciences except economics were rated least useful if they were mentioned and yet many respondents wished they had taken more social science courses. The apparent explanation for

this dichotomy is the current upsurge in recognition of the social problems and the lack of relevance of the earlier social science courses. Economics as a general subject was also judged least useful by some respondents, but resource economics was valued by many and was ranked sixth among those that respondents wished they had added or taken in greater depth.

Less divergent were the opinions about humanities and the liberal arts. This set of subjects ranked second among those listed as least useful. A very small proportion of the respondents valued them highly, and some explained that courses in music and literature were especially useful in their life but not in their professions.

Courses in administration were rarely mentioned as useful but ranked seventh among the subjects that the respondents wished they had taken. Apparently such courses were seldom taken by the respondents but are needed, especially by many of the older fishery scientists.

VOLUNTARY OPINIONS REGARDING THE CURRICULUM

The respondents were asked to comment freely on the training of fishery scientists, and about one-third did so. The opinions were classified and the categories ranked (Table 3).

Most of the opinions expressed related to the need for extending and improving the curriculum. These include six of the eight items enumerated in Table 3, and these eight items include all comments mentioned by more than 2% of the respondents. The other two groups of comments indicate a desire for greater relevance and more practice and experience.

The prevailing views about improving the curriculum almost always suggested that something should be added but rarely suggested what should be eliminated. It follows that more effort should be made to relate the curriculum to future roles of fishery scientists as well as to provide ways of acquiring the courses used by only a small proportion of the scientists through night school, seminars, or home study.

TABLE 3.—Voluntary opinions regarding the curriculum expressed by respondents and their ranking.

Opinion	Percent
Develop more technical skills	8
Develop more communication skills	7
Develop more business, administration skills	6
Include more environmental courses	6
Have greater relevancy to real problems in courses	6
Increase practice and experience	6
Have less specialization	5
Emphasize scientific methods	5

PROPORTION OF SPECIALIZED FISHERY COURSES IN THE CURRICULUM

The members of PFB were also asked for their opinions about the proportion of specialized fishery courses in the curriculum in various years with various terminal degrees.

The replies were highly varied, but the average opinion (Table 4) was that the beginning curriculum should contain very few specialized fishery courses and that the final years should contain 50 to 60% specialized fishery courses. The final years are, of course, the junior-senior years of the baccalaureate program and the graduate years of the master and doctorate programs. Clearly the average opinion indicated a different upper class curriculum for the student who ends with a baccalaureate than for the student who plans graduate work at the outset.

TABLE 4.—Average opinions of the percentage of the fishery curriculum that should be comprised of specialized fishery courses.

	Terminal degree		
	B.S.	M.S.	Ph.D.
N	279	209	195
Lower class	16	10	10
Upper class	52	27	24
Graduate		56	59

GROUP COMPARISONS

The diverse opinions about the subjects suggest immediately an inquiry into the relation of the subjects' usefulness to the respondents' professional activities. The respondents can be divided into groups according to position, title, employer, activity, kind of fishery, final degree, major topic of study, and number of years since last degree (Table 1). The groups that can be

chosen by students during their undergraduate years deserve special examination.

Highest Degree

A major decision that a student should make sometime during his upper class years is whether to continue with graduate work. In the past these choices were probably between research or teaching and management or administration, but the careers have not been as neatly divided, nor are they likely to be in the future as more Ph.D.s go into management and administration.

Respondents holding baccalaureate and doctorate degrees differed primarily in their opinions regarding the basic vs. applied sciences. A higher proportion of those with a doctorate degree than of those with a baccalaureate rated biology, mathematics, and foreign language as their most useful subject. More would have added advanced biology, mathematics, and geology. More would improve the curriculum by giving more attention to scientific methods and less to specialization. A higher proportion of those with only a baccalaureate rated fisheries-fishery biology, fishery management, wildlife science, and biostatistics-population dynamics-computer sciences as their most useful subject, and a higher proportion would have added ecology, fisheries-fishery biology, administration, English composition, and public speaking. They suggested especially increased practice or experience and addition of communication and administration skills to the curriculum. The average opinions of those with a master as their highest degree were frequently intermediate between those with a baccalaureate and those with a doctorate except that a higher proportion of them listed advanced biology, advanced chemistry, physics, and forestry as the least useful subject and would have added economics and administration more often than either of the other groups. A higher proportion of them also suggested improving the curriculum by adding environmental courses.

Activity

The members of PFB were asked in the questionnaire to indicate the proportion of time spent in research, management, teaching, administration, or other activities. Almost all divided their time between two or more of these categories, and it was decided to separate the opinions of those who said they were devoting 40% or more of their time to any one activity. These activities might be chosen by the student; therefore, the professional opinions would be useful to him.

The researchers valued quantitative methods more highly than the others did. A larger proportion of this group listed mathematics-calculus and biostatistics-population dynamics as the most valuable subject, and social sciences and humanities-liberal arts as the least valuable. The proportion of them that recommended increased practice and experience in the curriculum was also greater.

The managers valued natural history and communications. A larger proportion of them rated ichthyology-systematics, ecology, fishery management, and public speaking as the most valuable subject. A smaller proportion of them than of the other two groups rated mathematics-calculus as the most valuable subject. A larger proportion of them also ranked biology, advanced chemistry, and physics as the least valuable course, but add aquacultural sciences, and recommended that courses have greater relevance to real life problems and that the curriculum include more communication skills.

The administrators valued general biology and wished they had taken more courses in the social sciences and administration. A larger proportion of them rated biology and invertebrate zoology-marine biology as the most valuable subject, wished they had taken more biology, social sciences, and administration, and recommended that the curriculum be improved by the addition of administration courses.

The teachers (although the sample was small) tended to be extreme in their opinion of several subjects. A larger proportion of them ranked the basic sciences—zoology, ecology, advanced zoology, chemistry, and oceanography-limnology—as the most valuable subject and a smaller proportion of them rated the applied biological sciences, the social sciences, and public speaking as the most valuable subject. Somewhat anomalously, a larger proportion of them recommend-

ed that the courses have greater relevance to real problems, emphasize more technical skills, more scientific methods, and be less specialized.

Type of Fishery

A preponderance of the fishery scientists work mostly with either recreational fisheries or commercial fisheries. Most of those working for the state fishery or fish and game agencies, the Bureau of Sport Fisheries and Wildlife, and the nonfishery agencies were concerned with recreational fisheries; and most of those working for the National Marine Fisheries Service and for universities were concerned with commercial fisheries. The balance included a few who divided their time equally between recreational and commercial fisheries and some who were extensively engaged in environmental problems.

The recreational fishery scientists valued natural history and environmental and communication subjects. A larger proportion of them than of the commercial fishery scientists rated ecology, ichthyology-systematic zoology, invertebrate zoology-marine biology, fishery management, oceanography-limnology, aquacultural science, and public speaking as their most valuable subject, wished they had added such subjects, and suggested that courses should have greater relevance to actual problems and the curriculum should have more environmental courses.

The commercial fishery scientists valued quantitative methods, fisheries, and economics. A larger proportion of them rated mathematics-calculus, fisheries-fishery biology, biostatistics-population dynamics-computer use, and economics as their most useful subject, wished they had added these subjects, and commented on the need to improve the curriculum by the addition of business and administration courses.

Fisheries vs. Biology-Zoology Major

More than 90% of the PFB respondents had majored in either fisheries, biology, or zoology. Those who had majored in fisheries frequently had minored in biology, zoology, or chemistry. Regardless of major, however, the distribution among duties and types of fisheries was almost the same.

A higher proportion of the fishery majors listed ichthyology-systematic zoology, mathematics-calculus, fisheries-fishery biology, fishery management, wildlife management, English composition, and public speaking as their most valuable subject, wished they had taken more ecology, ethology, psychology, and economics, and commented on the need for courses with greater relevance to real problems and on the need to add environmental courses.

On the other hand, a larger proportion of the biology-zoology majors listed ecology, physiology, and invertebrate zoology-marine biology as their most valuable subject, wished they had taken more calculus, geology-hydrology, and fishery management, and suggested less specialization in the curriculum.

Shifts in Opinions with Passage of Time

Information on the years since the last degree enabled a breakdown into three decade groups <10, 10-19, and >19 years with considerable numbers in each. Interpretation of the different opinions is difficult, however, because of changes in curricula, changes in status of the respondents with age, and dimmed memories.

The oldest group tended to cling to the traditional sciences and communications. A larger proportion of them rated biology, zoology, botany, chemistry, physics, English composition, and public speaking as the most valuable subject, wished they had had more of these subjects, and wished they had added more administration.

On the other hand, the youngest group valued more highly the environmental, quantitative, and applied sciences. A larger proportion of them rated ecology, ichthyology-systematic zoology, fishery management, and biostatistics-population dynamics as the most valuable subject. They also had stronger negative opinions; a larger proportion of them listed advanced zoology, chemistry, physics, economics, and humanities-liberal arts as the least valuable subject (although a slightly larger proportion of the intermediate age group rejected humanities-liberal arts).

COMPARISON OF OPINIONS FROM PFB AND FISH CULTURISTS

Few members of PFB were concerned with any kind of aquaculture; therefore a similar questionnaire was submitted to people in the western United States who were on a mailing list (December 1968) for the Northwest Fish Culturists Conference. The number of respondents was much smaller, perhaps because a considerable proportion of the fish hatchery superintendents lacked college degrees, but usable answers were obtained from 16 fish cultural supervisors and 19 fish cultural researchers. The first group included 7 without a baccalaureate degree, 9 with, and none with a higher degree. Of the second group all had baccalaureate degrees, 5 had master, and 7 doctorate degrees; 15 were employed by government laboratories.

A larger proportion of the fish cultural supervisors than of the PFB members rated physiology, oceanography-limnology, aquacultural sciences, and hydraulic engineering as the most useful courses. They found basic mathematics very useful but not higher mathematics or biostatistics-population dynamics, but many wanted to add courses in the latter. They listed English composition and public speaking as the most valuable course about as often as the PFB members did. Above all they wished they could have added more courses in the aquacultural sciences.

The fish cultural researchers valued subjects much differently from either the total PFB members or the PFB researchers. A larger proportion of them listed physiology, advanced biology, chemistry, advanced chemistry, physics, and the aquacultural sciences as their most valuable subject, and botany, sociology, and economics as their least valuable. Fewer of them than of the other two groups rated biostatistics-population dynamics as their most valuable subject but many wished they had taken more. Above all they wished they had taken more physiology, advanced chemistry, and aquacultural sciences.

COMPARISON OF OPINIONS FROM PFB AND STUDENTS

The questionnaire circulated to the PFB was also given to undergraduate and graduate seminar groups in the College of Fisheries of the University of Washington. Replies were received from 20 undergraduate and 28 graduate students.

There was a notable diversity of opinion among the undergraduates. A relatively large proportion listed the following subjects as the most valuable course and a similarly large proportion rated them as their least valuable: research methods, advanced chemistry, physics, fisheries-fishery biology, fishery management, and biostatistics-population dynamics. Because of this diversity, no critical comparison of their opinions with those of PFB members is possible; but they seemed to value zoology and communication courses much less than PFB members and aquacultural sciences more than PFB members.

The graduate students were much closer to PFB members in opinions and differed largely from them in only a few subject areas. A larger proportion of them rated physiology, biostatistics-population dynamics, and aquacultural sciences as the most valuable course, whereas fewer of them included chemistry and communications as the most valuable course. They differed especially with regard to communications; they had no understanding of its importance.

SUMMARY AND CONCLUSIONS

1. No single curriculum is ideal for training in fishery science. The field has become much too broad and includes too many specialties that each require a high level of training. The specialization is expected at graduate level, of course, but is desirable even at undergraduate level if students can anticipate either the graduate work or the type of job they will enter.

A corollary of the above conclusion is that a person with a terminal baccalaureate degree should not be a dropout from a research-oriented, two-degree or three-degree program. A majority of the jobs in fishery science has been held and probably will continue to be held by people with only a baccalaureate degree. Some of these jobs will be major administrative, decision-making jobs with rewards equal to those that will be open to holders of a doctorate degree.

2. A biology or zoology undergraduate major may be good preparation for graduate work in fisheries, but it is relatively poor preparation for a job. Advanced biology courses in general are much less useful than courses in English composition, public speaking, fishery science and management, and the quantitative sciences.

3. Student and faculty opinions about curricula are probably not the best guides. Both differ substantially from the opinions of a majority of the nonteaching professionals in the field, especially in their evaluation of subjects that develop the ability to deal with people.

4. Courses in the social sciences, humanities, and liberal arts have not been as useful as people now want them to be. With a few exceptions these subjects were characteristically among those listed as the least useful. The exceptions are important as indication of needed improvements because they include courses in resource economics and administration—both public and business. These are courses that are relevant to real problems, and it would appear that many social sciences-humanities-liberal arts courses have not been relevant hitherto.

5. The high value of general courses in science, both basic and applied, and the mixed value of advanced courses indicate the importance of teaching the general courses especially well.

6. There are advantages in a fishery education that is interrupted by periods of work. The student can form definite opinions about specialties that he needs for the job that he has or wants. In addition almost everyone can benefit from refresher courses that cover new developments.

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EFFECT OF CROWDING ON RELATION BETWEEN EXPLOITATION AND YIELD IN *TILAPIA MACROCEPHALA*

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ABSTRACT

An experiment was performed to assess the effect of crowding on yield in *Tilapia macrocephala*. Populations of nearly equal number and weight were started in control (155.2 liter) and test (77.6 liter) tanks. Food amounts and environmental attributes other than space were the same for both tanks. Each of the two populations was exploited—first at a bimonthly rate of 10% for 14 months, then at a bimonthly rate of 25% for 10 months.

Equilibrium yields at each rate for each tank (four points) were fitted with a Fox exponential surplus-yield model. Deviations from this general population curve showed that yields were greater for the larger tank at the 25% rate and greater for the smaller tank at the 10% rate. This is believed to result from the fact that the entire yield came from growth at the lower rate whereas part of the yield came from recruitment at the higher rate. A low rate of conversion of food to fish (18%) is believed to be due to the large proportion of liver in the diet.

Current interest in aquaculture suggests an imminent increase in the holding of fish in restricted enclosures. Such holding, particularly at high densities, provides the fish with a drastically altered environment as compared with their native habitat. Some of the effects are undesirable, as is only too well known to hatchery men. Metabolic wastes accumulate rapidly and some communicable diseases spread easily among enclosed populations. There may also be undesirable effects due to reduced area for spawning—for example, spawning fish that are close together may use more energy defending their territory against the intrusion of other fish than spawners that are farther apart. Effects of crowding can also be beneficial, such as increased growth rate with less expenditure of energy in swimming.

The purpose of the experiment described here was to investigate one class of results from crowding—those related to the yield in self-sustaining populations. Of many possible experimental animals, *Tilapia macrocephala* belongs to a genus which is already important in pond culture. This species is small enough to raise in laboratory tanks and has reasonably rapid reproduction and growth. A conventional control-test design was adopted in which the control population was in a tank that had been demonstrated as being of suitable size for *T. macrocephala*. The test population was in a tank exactly one-half the size of the control tank. Food, light, temperature, and initial populations were kept as nearly identical as possible.

MATERIALS AND METHODS

Two conventional glass-wall aquarium tanks were used. The water mass in the control (larger) tank (L) had a volume of 155.2 liters, with approximate dimensions 39 by 90 by 44 cm. Volume of the test (smaller) tank (S) was one-half that of L, or 77.6 liters. To keep proportions the same, linear dimensions of S and its equipment were $1/2^{1/3}$ those of L.

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Tank L was provided with two fiber-charcoal filters, each with an electric pump delivering 2,800 ml per min; tank S had one of these.

Aeration was by one airstone in tank L and two in tank S.[2] Oxygen concentrations varied from 4.4 to 7.4 ppm for L and 2.4 to 7.2 ppm for S.

Illumination was by overhead pink fluorescent lamps, which screened out violet-blue light, found by Perlmutter and White (1962) to be lethal to some fish eggs. Lights were controlled by an automatic switch, turned on from 6 AM to 6 PM each day.

Each tank had shelter in the form of cords suspended from plastic floats. Forty-four cords 30 cm long were attached to a 49- by 15-cm float in tank L; numbers and dimensions of the shelter were proportional in tank S. A floating fiber brush type shelter, 4 cm in diameter by 25 cm long, was in L, and a proportional one was in S. The back, one side, and part of the front of each tank were rendered opaque with black plastic; the front area was 44 by 20 cm in L and proportional in S.

Refuges for young fish were enclosed at the end of each tank by fences consisting of 5-mm diameter plastic rods spaced 3 mm apart. The enclosed area was 14 cm wide in L and proportional in S. Aquarium gravel was placed in the bottom of each tank for nesting activity.

Both tanks were maintained at room temperature, which was thermostatically controlled except that cooling was not available in the summer. Weekly mean temperatures were 24 ± 2°C for both tanks.

Fish were fed daily according to a fixed schedule (Table 1). Uneaten food, feces, and other detritus were siphoned out daily, and two-thirds of the water mass was changed each week, using tap water brought to tank temperature. Charcoal and fiber in the filters were changed once weekly.

Populations were counted and weighed every 2 months. Since *T. macrocephala* is a mouth breeder, it was not desirable to handle the fish more often. Aronson (1949) stated that the mean spawning interval for the species was 15 days, so the counting interval was about four brood intervals. Exploitation was performed at the time of counting by removing the tenth or fourth fish for 10% and 25% exploitation rates. Weighing was done by draining fish in a net, placing them in a weighed container with water, weighing the container with fish, and subtracting the tare.

TABLE 1.—Amounts (grams) of food placed in each tank.

Day of week	Trout pellets		Tropical fish food	Liver	Total
	Moist	Dry			
Sunday	6.0	1.5	1.5	--	9.0
Monday	1.5	1.5	0.9	9.0	12.9
Tuesday	1.5	1.5	0.9	9.0	12.9
Wednesday	1.5	1.5	0.9	9.0	12.9
Thursday	1.5	1.5	0.9	9.0	12.9
Friday	1.5	1.5	0.9	9.0	12.9
Saturday	1.5	1.5	0.9	9.0	12.9
Total	15.0	10.5	6.9	54.0	86.4

Exploitation started in December 1967, with 42 fish weighing 1,148 g in S and 45 fish weighing 1,167 g in L (Table 2). These fish were either survivors or descendants of a shipment of 10 adults and 50 young fish received on 10 February 1966 by air from the Honolulu Biological Laboratory of the Bureau of Commercial Fisheries (now National Marine Fisheries Service).

Although numbers of fish declined at the 10% bimonthly exploitation rate (Figure 1), biomass remained relatively constant (Figure 2) and no evidence of recruitment was observed. To determine if recruitment would occur at a lower biomass, the exploitation rate was increased to 25% at month 16 and was continued at that rate until the end of the experiment. It will be shown below that recruitment did occur under the higher exploitation rate.

RESULTS

VITAL PROCESSES

Significant results from exploitation experiments require that recruitment and growth occur during the course of the experiment. It is also desirable to know whether natural (nonfishing) mortality was occurring. Evidence relating to these vital processes can be obtained by exam-

[2] Although these numbers may appear to be reversed, they are as used. The oxygen concentrations show that they provided approximately equal aeration.

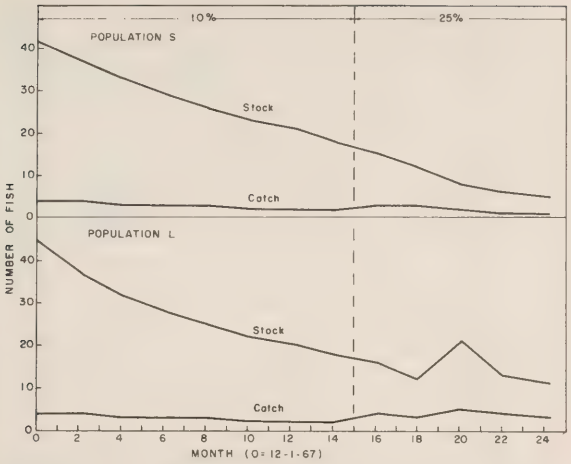

FIGURE 1.—Bimonthly stocks and catches, numbers, *Tilapia macrocephala*, 77.6-liter (S) and 155.2-liter (L) tanks. Percentages indicate target bimonthly exploitation rates.

ining net changes in number (R_{INT}) during the intervals between counts (Table 3).

Recruitment is defined here as survival of young fish to the size that could not pass through the 3-mm openings of the refuge fence. On this basis, no recruitment was apparent during the period of 10% exploitation, months 0-14 (Table 3). However, it is possible that some did occur, balanced by unrecorded mortality. Deaths not recorded are indicated by negative values of R_{INT} (Table 3). Also, it is almost certain that spawning occurred in which the resulting young were victims of cannibalism before reaching recruit size. Positive values of R_{INT} after month 14 show that recruitment occurred in both S and L under the 25% exploitation rate, with recruitment in L about double that in S.

Growth of individual fish can be detected by observing concurrent changes in numbers and biomass. Growth was demonstrated from month 0 to month 12.3, when biomass increased and numbers decreased in both S and L (Table 2, Figures 1 and 2).

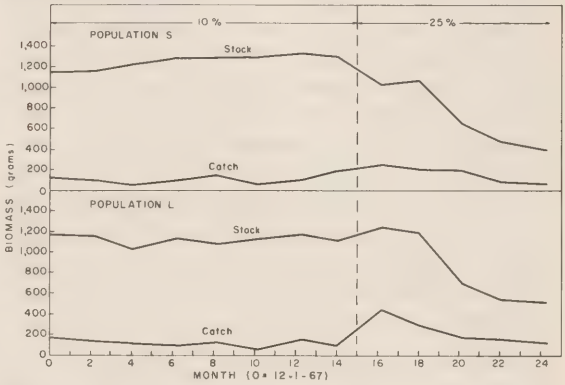

FIGURE 2.—Bimonthly stocks and catches, weights, *Tilapia macrocephala*, 77.6-liter (S) and 155.2-liter (L) tanks. Percentages indicate target bimonthly exploitation rates.

TABLE 2.—Population[1] and catch, *Tilapia macrocephala*, in two sizes of tanks during bimonthly exploitation.

Target exploitation rate[2]	Month[3]	S—77.6-liter tank				L—155.2-liter tank			
		Number		Weight (g)		Number		Weight (g)	
		Stock	Catch	Stock	Catch	Stock	Catch	Stock	Catch
0.10	0.0	42	4	1,148	132	45	4	1,167	178
	2.2	37	4	1,159	103	37	4	1,159	143
	4.0	33	3	1,216	47	32	3	1,026	122
	6.2	29	3	1,293	100	28	3	1,142	104
	8.1	26	3	1,288	153	25	3	1,076	126
	10.1	23	2	1,299	63	22	2	1,137	62
	12.3	21	2	1,338	109	20	2	1,181	160
	14.0	18	2	1,308	205	18	2	1,120	101
0.25	16.2	15	3	1,028	262	16	4	1,246	450
	18.0	12	3	1,080	216	12	3	1,195	297
	20.1	8	2	676	211	21	5	725	183
	22.0	6	1	496	102	13	4	562	156
	24.3	5	1	419	81	11	3	529	134

[1] In the 77.6 liter tank the population was replaced after accidental mortality at month 19. Also, sex ratio was changed from 1 male:5 females to 3 males:3 females at month 21.2.
[2] Because of the relatively small numbers of fish, the effective exploitation rates varied considerably from these. In fitting the population model, the effective rates in terms of weight were used.
[3] 0 = December 1, 1967.

Both recorded and unrecorded natural mortalities occurred. Recorded mortality represented finding of dead fish in the tanks. Unrecorded mortality, as mentioned above, is demonstrated by negative values of R_{INT} (Table 3).

CHANGES UNDER EXPLOITATION

Responses of the populations varied with exploitation rate. At the 10% rate, numbers in each population declined while biomass remained relatively constant (Figures 1 and 2). At the 25% rate, both numbers and weights declined. Further consideration of stock changes will be limited to data of biomass, since the biomass curves are more regular than those of numbers and represent both recruitment and growth. It is evident that the initial rise in weight of catch at the 25% rate was due almost entirely to cropping off the biomass accumulated at the 10% rate (Figure 2). The response of both populations to an increase in exploitation rate thus followed classical conceptions based on theoretical grounds (for instance, those of Thompson and Bell, 1934).

EQUILIBRIUM YIELDS

In a relatively short experiment, such as this, covering only 13 exploitation periods, the attainment of complete equilibrium at either of the exploitation rates is obviously impossible. The last two exploitation periods at each rate encompass relatively small changes in stock and catch (Figure 2); they will thus be considered equilibrium periods for the purposes of the analyses reported below.

POPULATION MODEL

The exponential surplus-yield model of Fox (1970) is simple to fit and has been found suitable for experimental populations with short brood intervals (Silliman, 1971); it was therefore chosen for use with the data from the *T. macrocephala* experiment. Ideally, the model would be fitted to S and L separately. The regression method employed for fitting does not perform well when only two points are available. There is no opportunity for compensating errors, and slight errors are greatly magnified when the regression is extrapolated to the Y-intercept to estimate the maximum stock. Also, since there are zero degrees of freedom, there is no way of assessing variability.

The above difficulties can be circumvented by fitting a single general curve to both populations. For individual population characteristics, deviations from the general curve can be studied. Four points were available for fitting the regression line—two from each population (Figure 3). The fit seems reasonably good for an experiment of this type.

TABLE 3.—Recruitment and unrecorded mortality, *Tilapia macrocephala*. $R_{INT} = P_{n+1} - P_n + M_{INT} + C_{INT}$, where INT is interval between counts n and $n+1$, R is net change,[1] P is stock, M is recorded mortality, and C is catch, all in numbers.

Interval (months)	R_{INT} for:	
	Population S—77.6-liter tank	Population L—155.2-liter tank
0- 2.2	−1	−2
2.2- 4.0	0	−1
4.0- 6.2	−1	0
6.2- 8.1	0	0
8.1-10.1	0	0
10.1-12.3	0	0
12.3-14.0	−1	0
14.0-16.2	+1	0
16.2-18.0	0	0
18.0-20.1	+4	+12
20.1-22.0	0	−2
22.0-24.3	+3	+3

[1] $R_{INT} > 0$ indicates recruitment of at least the indicated number of fish, $R_{INT} < 0$ indicates unrecorded mortality of at least the indicated number, and $R_{INT} = 0$ indicates either no recruitment and unrecorded mortality, or the two exactly balanced.

COMPARISON OF YIELDS

Deviations from the general curve (Figure 3) may be considered with respect to the crowding effect. It is seen that at the lower exploitation rate (10% target) and larger population, the population in the smaller tank (S) has a large positive deviation whereas that in the larger tank (L) is close to the curve. Conversely, at the higher exploitation date (25% target) and

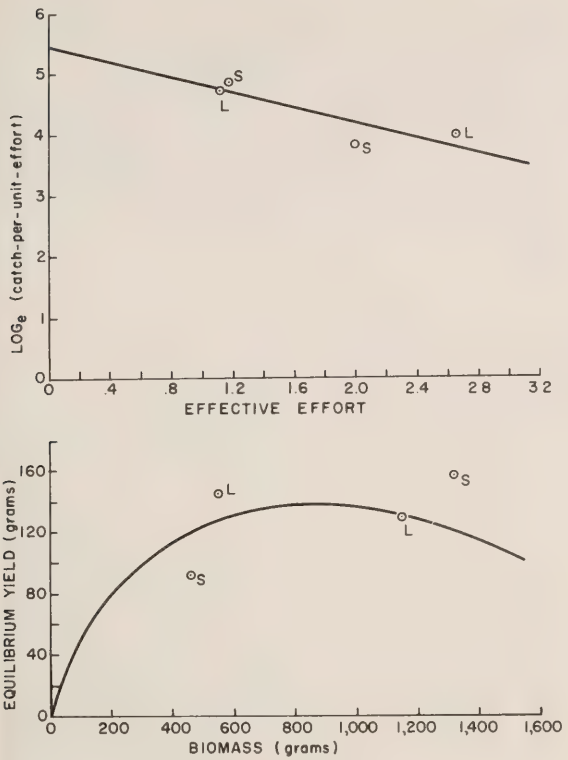

FIGURE 3.—Effort-CPUE line (least squares fit) and biomass-yield curve, fitting of Fox (1970) model. CPUE assumed proportional to population size. L indicates population in 155.2-liter tank and S in 77.6-liter tank.

smaller population, L has a positive deviation and S a negative.

An explanation for this seemingly paradoxical finding may be found in the source of the yield at each exploitation rate. At the lower rate, during months 0-14, the populations were large and no recruitment occurred (Figure 2, Table 3). The yield that did occur, then, resulted entirely from growth. Under the higher exploitation rate prevailing during months 16-24.3, the population was smaller and recruitment did occur (Figure 2, Table 3), furnishing part of the yield. Growth could have been retarded in the larger tank by greater expenditure of energy in swimming. Recruitment could have been favored in that tank by psychological factors controlling spawning, by greater opportunity for newly released young to escape cannibalism, or by a combination of these factors.

The finding of greater growth in the smaller tank is in contradiction to the conclusions of Chen and Prowse (1964) for *T. mossambica*. Examination of their data, however, shows that these conclusions were based on results from their largest ponds (0.10-0.40 ha) after a year of growth. Data comparing their smaller ponds were available only to 6-months' growth and are less clear cut. For instance, at 6 months their 0.04-ha pond showed greater growth than their 0.20-ha pond. Even their smallest pond (0.004 ha and 76 cm depth) had a volume of 31,000 liters, or 200 times that of the larger tank in the *T. macrocephala* experiments. With a different species (even though in the same genus) and such a vast difference in size of habitat it is perhaps not surprising that their findings are at variance with those reported here.

In both the present experiment and that of Chen and Prowse, the term "crowding" can be used only in a relative sense and not in the sense of lack of space to move about. Assuming the fish have the same density as water (nearly true), the maximum population in the smaller tank of the present experiment occupied only 1.72% of the water. The maximum concentration in Chen and Prowse's experiments was 0.02%. Thus, whatever effects occur must result from such factors as relative distance swum or sociological phenomena, like aggression. Chen and Prowse chose the latter, although it is a bit difficult to imagine when there are 2 or less kg of fish per 10,000 liters of water.

Finally, yields may be compared as measures of conversion[3] of food to fish flesh. The maximum bimonthly sustainable yield from the general population curve (Figure 3) is about 140 g (calculated value, 137.8 g). Food provided during each 2-month period weighed 749 g (8⅔ weeks × 86.4 g weekly total fed, as shown in Table 1). Apparent conversion was thus 18%.

The above results may be compared with those from the growth experiments of Swingle (1960)

[3] Used here in the sense of net growth in weight (= sustainable yield) expressed as a percentage of weight of food made available to the population.

in 0.40-ha ponds. His data are not directly comparable, however, as he fertilized the ponds in addition to feeding the fish. A rough correction may be made by subtracting growth achieved in unfed groups of fish. By doing so, a mean of 42% is obtained for *T. mossambica* in seven experiments starting with brood stock and lasting a single growing season. The much poorer showing of *T. macrocephala* in the present experiment is believed to be partly due to the large proportion of liver included in the diet (Table 1). Substantial amounts of uneaten liver were often removed from the tanks during daily cleaning. Also, the population density in Swingle's ponds was about two orders of magnitude less than in the present experiment, which may bear on the difference in food conversion. His ponds were about the size of the larger ones used by Chen and Prowse (1964), so their finding of greater growth in larger ponds may account for some of the superiority in growth found by Swingle.

ACKNOWLEDGMENTS

My thanks are due to Dr. Ralph Hile for suggesting an experiment to study space effects. Initial stocks were contributed by the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory through the kindness of Heeny S. H. Yuen and Robert T. B. Iversen. George F. Slusser developed the diets and experimental procedures. The populations were maintained by Martin G. Beam, Jimmy R. Chrnaoski, and Judy A. Trauth.

As part of the O. E. Sette dedicatory volume, I gratefully dedicate this small contribution to him. He was my first research supervisor (1938-45), and I owe a very great deal indeed to his encouragement, advice, and instruction during those formative years of my career.

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VARIATIONS IN SIZE AND LENGTH COMPOSITION OF ATLANTIC MENHADEN GROUPINGS

FRED C. JUNE[1]

ABSTRACT

This paper gives estimates of size (weight) and length composition of summer schools and fall school-aggregations of Atlantic menhaden based on single-set purse-seine catches and accompanying catch samples obtained in 1955-62. The data show that the fish school by length and the average size of summer schools decreases as the apparent abundance of fish in a given area of the coast decreases. The significance of the school concept in the study of the dynamics of the population and the effects of fishing upon it are discussed, and additional avenues of research are suggested.

The Atlantic menhaden, *Brevoortia tyrannus*, is a schooling fish that occurs in the western Atlantic Ocean from Nova Scotia to Florida and is the object of a purse-seine fishery over most of its range (Reintjes, 1969). The fishery is based on seasonal appearances of the fish schools in shallow waters overlying the inner half of the continental shelf (Roithmayr, 1963). Fishermen and aerial fish spotters, who locate and assist in the capture of menhaden, have a working knowledge of school size, composition, and behavior, but there exists little quantitative information on these and other aspects of the schooling phenomenon. Of primary interest to the fishery biologist are the degree to which the fish school by size, the relationship between size of schools and size of fish within schools, and the variation in size of schools in relation to changes in abundance of the fish and to fishing. These aspects of Atlantic menhaden schooling are the subject of this paper.

The nature of density and fishery-related changes in the schooling of various pelagic marine fishes is not well understood, but sufficient evidence was put forward by different workers to indicate insight into the importance of this behavioral phenomenon. The significance of the school concept in the study of the dynamics of an exploited fish population whose members are grouped and differentially distributed by size was apparently first recognized by Thompson (1926) and further elaborated by Sette (1943) for the Pacific sardine (*Sardinops sagax*). Much of the quantitative information on fish schooling dynamics has come from work on tunas. Schaefer (1948) and Brock (1954), for example, discussed some implications of observed variations in the size of fish within and between schools in the design of a sampling system for yellowfin (*Thunnus albacares*) and skipjack (*Euthynnus pelamis*) tuna stocks, respectively. Orange, Schaefer, and Larmie (1957) and Broadhead and Orange (1960) offered evidence of fishery-related changes in the schooling dynamics of yellowfin tuna, while Brock (1962) considered implications of the interrelationship between the size and number of yellowfin tuna forming a school and the success of longline fishing. June and Reintjes (1959) established that the Atlantic menhaden also schools by size, and they concluded that the school is therefore the appropriate unit for sampling the size, age, and sex composition of the population. They further demonstrated seasonal and annual variations in the estimated number and geographical distribution of purse-seine sets on menhaden schools in a series of reports beginning with 1955 (June and Reintjes, 1959), and Roithmayr (1963)

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summarized these data for the years 1955-59. There has been no further elucidation of the schooling dynamics of this fish. This study pursues that objective.

SOURCES AND TREATMENT OF DATA

The basic data consisted of fishing logbooks maintained aboard menhaden vessels for use by the National Marine Fisheries Service and reduction plant records of daily vessel landings from 1955 to 1962. Of the single-set catches recorded in the logbooks, only those for which the "hailed" catch was within 10% of the plant weights were used in the analyses. Vessel landings at the reduction plants were converted to metric tons.

I assumed that each purse-seine set during the "summer fishery" (April-September) was made on a discrete school of Atlantic menhaden. Sets made on large aggregations of fish that appeared off Long Island in late September or early October (June and Nicholson, 1964) and off North Carolina in November and December were considered separately.

Despite the rigorous screening of fishing logbooks, several sources of error may have been involved in the identification of single-school catches and estimates of school size. Foremost of these are (1) a portion of a school may have escaped during capture, (2) a variable loss in weight from decomposition may have occurred within single-school catches of the same initial size (such losses would be proportionately greater during warmer weather and in catches made at the beginning of the fishing day), and (3) a single recorded set may have actually included more than one set. Items (1) and (3) would have a greater effect on the catch estimates, but there is no way of determining the extent of these sources of error in this study; item (2) must be considered a random factor.

Catch samples, which provided measures of fish size, were taken from daily vessel landings at reduction plants along the Atlantic coast (Figure 1) as part of a routine catch-sampling program begun in 1955 (June and Reintjes, 1959). Fish lengths were grouped in ½-cm classes. The mean length, variance, and standard deviation and the mean weight, in grams, of fish in each catch sample were computed.

The number of fish within a single-set catch was determined by dividing the weight of the catch by the mean weight of the fish in the catch sample. A catch sample was obtained from 275 single-school catches during the summer fishery and from an additional 64 single-set catches from the large fall aggregations of fish off Long Island (23 sets) and North Carolina (41 sets).

Detailed logbook information and accompanying plant weights were available for 2,643 single-school summer catches and an additional 286 single-set fall catches off Long Island (138 sets) and North Carolina (248 sets). The number of single-school summer catches for which there were data constituted about 1% of an estimated 240,000 purse-seine sets made during the 8 seasons. Except for 1961 and 1962, when a combined total of only four single-school summer catches were recorded for the South Atlantic Area, single-set catches were taken throughout the range and period of fishing and are therefore believed to be representative of the schools or larger aggregations of fish into which the population was divided.

SEASONAL GROUPINGS OF THE FISH

Examination of 2,643 single-school summer catches indicated wide variation in school size (weight). A plot of the combined frequencies of single-school catches for the 8 seasons, by 3-ton size classes (upper panel, Figure 2), shows a pronounced skewness in the distribution toward smaller catches, with the mode occurring in the 4- to 6-ton size class. Single-school catches ranged from 0.3 to 103 tons. The grand mean for the 8 seasons was 16.6 tons, with a standard deviation of 12.25 tons. The size-frequency distributions of single-school catches in individual seasons (lower panels, Figure 2) also were asymmetrical and, without exception, similar in shape to that of the combined data. The maximum frequency in every year fell in either the 4- to 6-ton or the 7- to 9-ton size classes.

Although there were exceptions in some years, larger schools were generally found in the north-

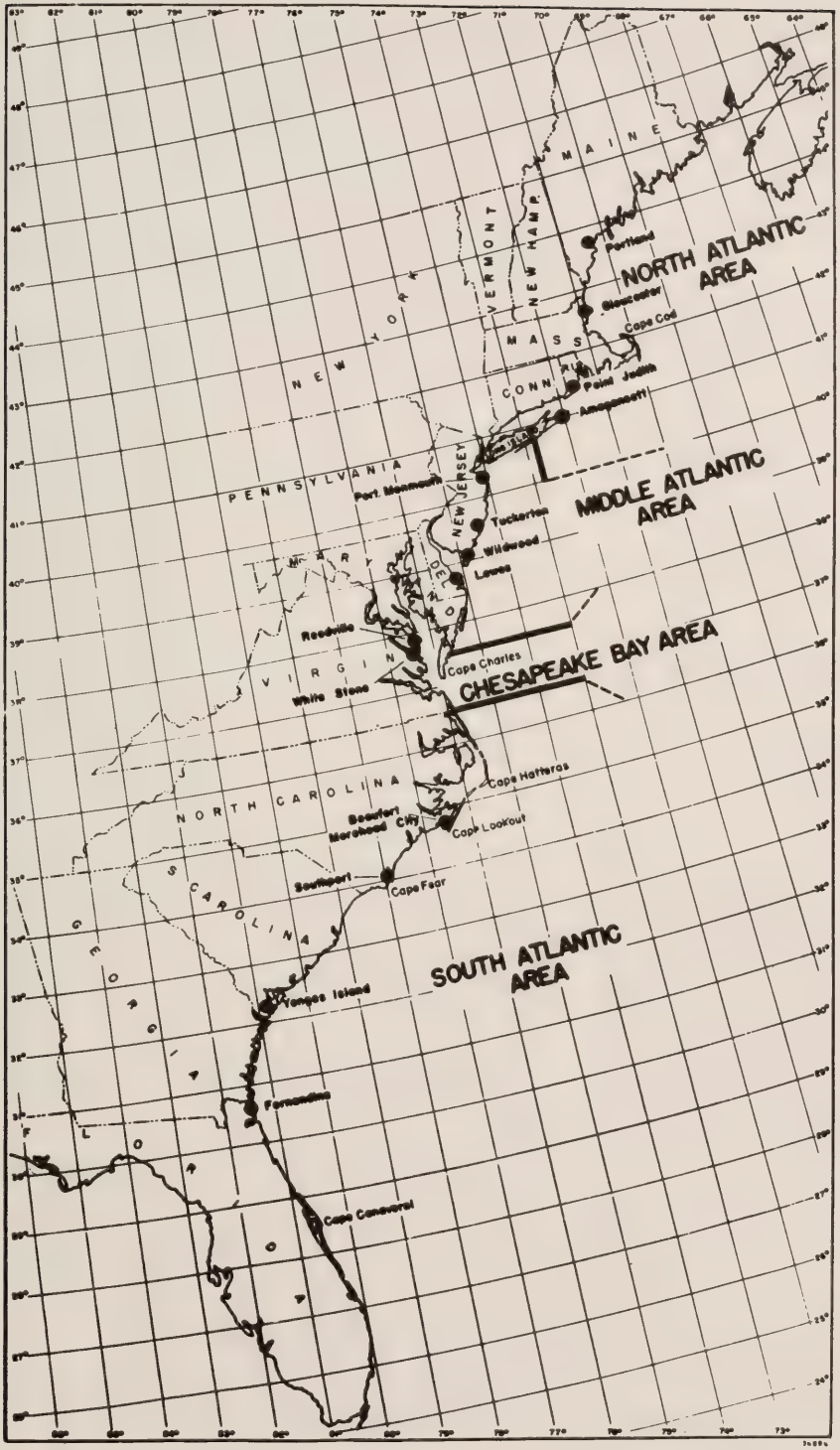

FIGURE 1.—Locations of reduction plants where Atlantic menhaden catch samples were collected and the four major geographical areas used in summarizing the biostatistical data.

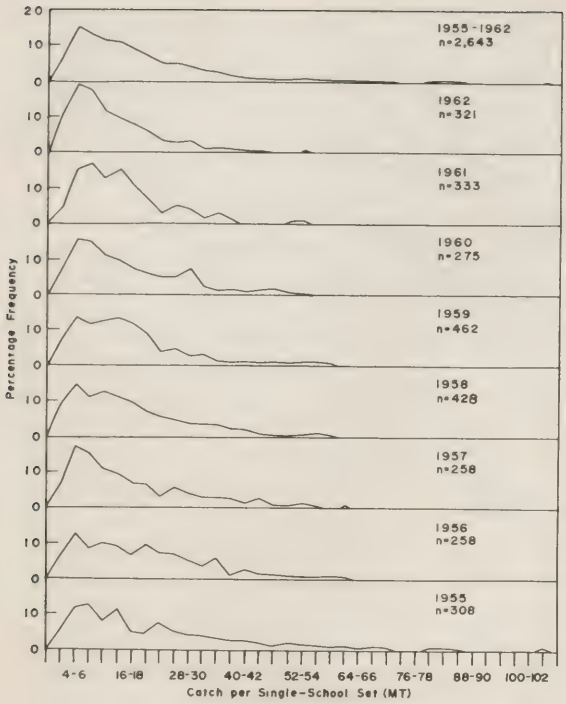

FIGURE 2.—Percentage size-frequency distributions of 2,643 single-school summer purse-seine catches of Atlantic menhaden, 1955-62.

ern part of the range during the summer, and progressively smaller schools occurred at lower latitudes. Comparison of the mean catch per single-school set within the four major areas of the summer fishery (Table 1) shows that schools in the North Atlantic Area averaged about 21 tons per set and 5 to 9 tons heavier than those in other areas. Schools in the Middle Atlantic Area were intermediate in size, averaging about 16 tons per set, while those in the Chesapeake Bay and South Atlantic Areas were smallest, averaging about 13 tons per set.

Size of summer schools declined from 1955 to 1962. The mean catch per single-school set in 1955 was 22 tons; it decreased and fluctuated around 16 tons from 1957 to 1960, and in 1962 it was only about half that in 1955 (Table 1). This decline was largely attributable to a reduction of school size in the North Atlantic and Middle Atlantic Areas, where decreases in the means amounted to about 40% over the 8-year period. In general, mean school size in the Chesapeake Bay and South Atlantic Areas fluctuated only slightly about their grand means. The high mean for Chesapeake Bay in 1955 resulted from several large single-school catches recorded at the beginning of the fishing season and probably is atypical (see also p. 704). Too few single-school catches were recorded in the South Atlantic Area in 1961 and 1962 (1 and 3, respectively) to be considered in calculation of these seasonal means. But in view of the relatively small size of single-school summer catches in previous years, additional data from this area in 1961 and 1962 would likely not have influenced the grand seasonal means.

There was a definite change in the grouping of the fish in autumn. In every year schools became noticeably reduced in number in surface waters of the Gulf of Maine in late August or early September, and during late September or early October large masses of fish, or "school aggregations,"[2] appeared off Long Island, only to disappear from these waters by mid or late

[2] To avoid confusion, the word aggregation is used in this paper in its general meaning and not as defined by Breder (1959).

TABLE 1.—Mean size of single-school summer catches of Atlantic menhaden from 2,643 purse-seine sets in the four major statistical areas, 1955-62. The number of sets used in calculating the means are given in parentheses.

Area	Year								Grand areal mean	Standard deviation
	1955	1956	1957	1958	1959	1960	1961	1962		
	metric tons									
North Atlantic	25.9(91)	26.4(75)	22.2(58)	18.8(78)	23.3(88)	19.2(80)	18.6(87)	15.8(48)	21.1(605)	15.32
Middle Atlantic	22.0(177)	17.3(154)	16.4(163)	16.7(258)	15.1(266)	15.4(163)	13.5(227)	13.2(163)	16.1(1,571)	11.72
Chesapeake Bay	21.9(19)	12.3(13)	11.0(19)	15.3(64)	12.4(28)	10.7(14)	12.0(19)	10.5(110)	12.8(286)	8.59
South Atlantic	11.5(21)	14.3(16)	10.3(18)	13.6(28)	12.5(80)	14.0(18)	---	---	12.6(181)	7.15
Grand seasonal mean	22.4(308)	19.5(258)	16.9(258)	16.7(428)	16.1(462)	16.2(275)	14.8(333)	12.7(321)	16.6(2,643)	12.25

October (Roithmayr, 1963; June and Nicholson, 1964; Nicholson, 1971a).

Single-set catches from fall school-aggregations, on the average, were larger than single-school summer catches. A plot, by 3-ton size classes, of 138 single-set catches made from large fall school-aggregations that appeared off Long Island shows a marked difference in the shape of the frequency polygon when compared with that of single-school summer catches in the North Atlantic Area (lower and middle panels, Figure 3). The ranges of the two distributions are nearly identical (3 to 102 metric tons for the fall school-aggregations), but the curve representing fall school-aggregations is more symmetrical and its mode considerably higher (40- to 42-ton size class) and in much closer agreement with the mean of the distribution (44.4 metric tons). Moreover, single-set catches from fall school-aggregations, on the average, were over twice as large, and the standard deviation of their frequency distribution was 1½ times greater than that of single-school summer catches in the North Atlantic Area (Table 2). Comparisons within years show the mean catch from fall school-aggregations to be from 1½ to 3½ times larger than the mean single-school summer catch in the North Atlantic Area.

Differentiation of summer schools and fall school-aggregations was also indicated by the fact that the mean single-school summer catch in the North Atlantic Area decreased over the 8-year period, whereas the mean single-set catch from the fall school-aggregations off Long Island generally increased (cf. Tables 1 and 2). Although the two seasonal catches were negatively correlated ($r = -0.228$), the coefficient has no statistical significance.

Following the disappearance of the fish from coastal waters of southern Long Island and elsewhere in October, large school-aggregations reappeared off the coast of North Carolina in November of every year. These aggregations were usually first intercepted by the fishing fleet in the vicinity of Cape Hatteras, N.C., and fished as they moved southwestward along the coast until they disappeared off Cape Fear, N.C., in December or early January (Roithmayr, 1963; Nicholson, 1971b).

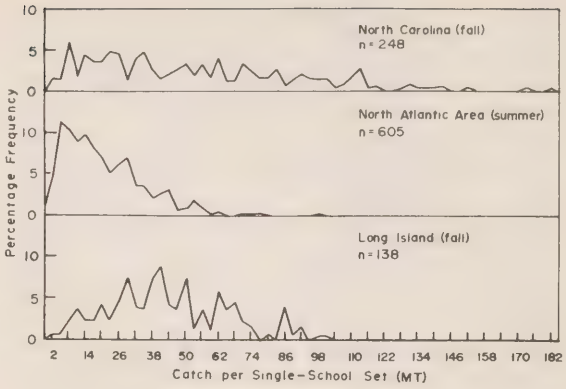

FIGURE 3.—Percentage size-frequency distributions of 138 single-set purse-seine catches of Atlantic menhaden from fall school-aggregations off Long Island (lower panel), 605 single-school summer catches in the North Atlantic Area (middle panel), and 248 single-set catches from fall school-aggregations off North Carolina (upper panel), 1955-62.

Single-set catches from fall school-aggregations off North Carolina, on the average, were the largest recorded along the Atlantic coast. A plot of 248 catches (upper panel, Figure 3) shows a range of 1.5 to 180 tons. The grand mean for the 8-year period was 54.2 tons, with a standard deviation of 37.63 tons. Thus, these catches, on the average, were from three to nearly five times heavier than single-school summer

TABLE 2.—Mean size of catches of Atlantic menhaden from 138 purse-seine sets on fall school-aggregations off Long Island and 248 sets on fall school-aggregations off North Carolina, 1955-62. The number of sets used in calculating the means are given in parentheses.

Locality	Year								Grand mean	Standard deviation
	1955	1956	1957	1958	1959	1960	1961	1962		
	metric tons									
Long Island	42.3(21)	37.8(12)	39.3(16)	34.1(10)	52.2(14)	47.3(26)	39.7(18)	54.3(21)	44.4(138)	21.77
North Carolina	34.8(29)	58.0(16)	46.1(43)	44.0(22)	58.6(32)	42.2(19)	69.7(72)	57.8(15)	54.2(248)	37.63

catches in the South Atlantic Area and were most similar in size to catches made 1 to 3 months earlier from school-aggregations off Long Island (Table 2).

In summary, the data presented demonstrate heterogeneity in the seasonal and areal grouping of Atlantic menhaden. Two basic groupings are evident: (1) summer schools, which are variable in size, comprised of discrete and independent clusters of fish, and differentially distributed over the range of the species, and (2) fall school-aggregations, which are large, but of undetermined size, and found only along their apparent southward migration route.

Questions immediately arise concerning the grouping of the fish following their disappearance off North Carolina through the time of their return northward migration in early spring. During this roughly 3-month period they are usually not seen at the surface. The spring movement seems to be largely over by the time that summer schools reappear in the inshore surface waters and become available to the purse-seine fishery. Inspection of first-of-the-season single-school catches suggested that some of these were larger than those taken immediately afterward, but the numbers of such catches were too few in most years to test this hypothesis statistically. Table 3, for example, gives available data on single-school catches during the first week of fishing in each major area (cf. Table 1). A plot of school size on time, however, indicated no clear relationship and in most years was similar to that shown in Figure 4. Thus, elucidation of the off-fishing season grouping of the fish awaits further study.

LENGTH OF FISH WITHIN AND BETWEEN GROUPINGS

There was a tendency for fish within summer schools to be of similar lengths, although the difference between the largest and smallest indi-

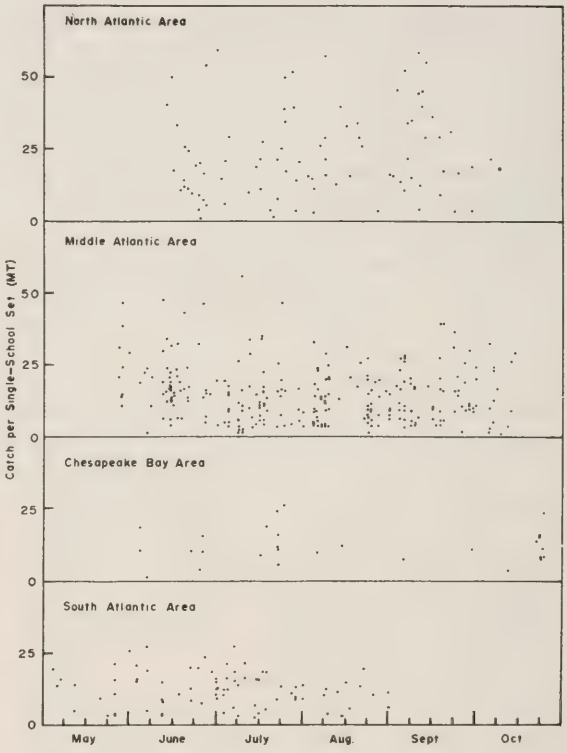

FIGURE 4.—Size of 462 single-school summer purse-seine catches of Atlantic menhaden in the four major statistical areas in 1959 plotted against time.

TABLE 3.—Size of single-school purse-seine catches of Atlantic menhaden made during the first week of the fishing season in the four major statistical areas, 1955-62.

Year	Area											
	North Atlantic			Middle Atlantic			Chesapeake Bay			South Atlantic		
	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean	No.	Range	Mean
		metric tons			*metric tons*			*metric tons*			*metric tons*	
1955	6	11-63	37.7	32	4-72	35.4	3	20-43	30.7	-	--	--
1956	6	7-49	29.2	12	3-47	19.6	4	4-35	17.8	-	--	--
1957	-	--	--	13	2-33	11.8	1	--	8.0	3	8-21	12.7
1958	2	12-32	21.7	3	10-23	16.0	-	--	--	-	--	--
1959	4	18-49	35.4	15	2-47	22.0	2	11-18	14.6	5	5-19	13.3
1960	3	17-41	29.4	3	10-34	23.9	-	--	--	-	--	--
1961	6	8-28	17.2	16	5-28	15.9	1	—	13.3	-	--	--
1962	3	7-30	17.5	14	7-57	23.0	3	10-29	22.8	-	--	--

viduals within a school was variable. The mean of the length range of fish within samples from 275 single-school summer catches was 5.8 cm, with a standard deviation of 2.11 cm; the range was 1.5 to 13.0 cm. The seasonal means ranged from 5.1 to 6.8 cm, with no trend indicated during the 8 years. These findings support Breder's (1959) generalization that the difference in size of fish that will form an acceptable school does not exceed 50%.

To determine if variations in the length range within summer schools were associated with the relative lengths of the members, I plotted the variance against the mean length of fish in samples from 275 single-school catches (Figure 5). The variances obviously are heterogeneous, with variation within schools being greater among fish that averaged over about 25 cm in length.

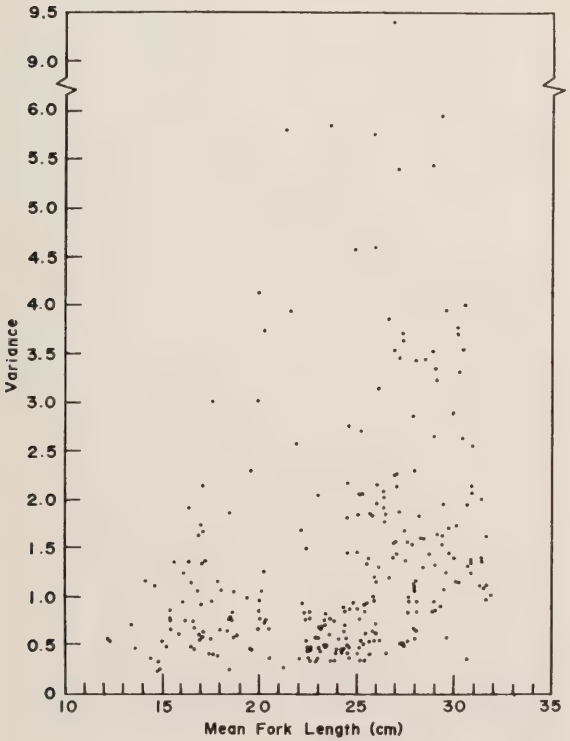

FIGURE 5.—Variance plotted against the mean of the length-frequency distribution of Atlantic menhaden in samples from 275 single-school summer purse-seine catches, 1955-62.

A plot of variances on time failed to show any trend within or between seasons. Thus, while summer schools of Atlantic menhaden are highly length-selective, schools of mixed lengths do occur, and variation seems to be greater within schools of larger fish than within schools of smaller fish.

The length range of fish within individual summer schools was less than the length range among schools inhabiting any given area of the coast, or of the population as a whole. In Figure 6, for example, are graphed the length-frequency distributions of fish in samples from 52 single-school catches made throughout the range of the summer purse-seine fishery in 1959. The least range in length within schools was 3.0 cm and the greatest 12.0 cm; the mean difference was 6.1 cm, with a standard deviation of 2.42 cm. In general, these data show that the lengths of fish found in the different areas of the coast varied considerably, and there was a decrease in

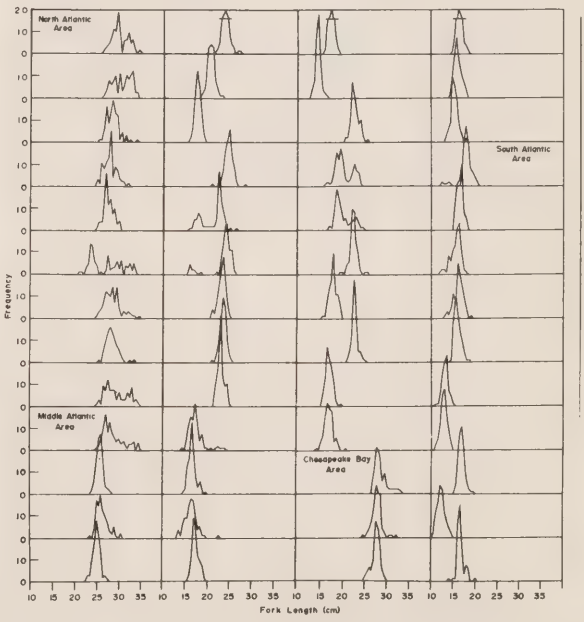

FIGURE 6.—Length-frequency distributions of Atlantic menhaden in samples from 52 single-school summer purse-seine catches in 1959. The samples are grouped by major statistical areas and arranged in order of decreasing latitude.

length with a decrease in latitude. But the important features of interest are the unimodality of most of the distributions, the decrease in variability within schools as the fish get smaller, and the comparatively narrow range of fish length within schools in contrast to the wide range of fish length within each area as a whole (cf. Nicholson and Higham, 1964). In the Middle Atlantic Area, for example, the length range within single-school catch samples varied from 3.0 to 10.1 cm, whereas the length range for the combined single-school catches sampled in that area was 21.5 cm (13.0 to 34.5 cm). So the segment of the population inhabiting any given area of the coast during the summer is evidently stratified, with each stratum comprised of discrete schools of fish grouped according to length.

Fall school-aggregations off Long Island consisted of large fish that were only represented in the North Atlantic Area during the summer. Length-frequency distributions of fish in samples from 23 single-set catches from these school-aggregations tended to be unimodal and contained relatively few fish under 25 cm (Figure 7). The range in length of fish within individual catch samples varied from 4.0 (28.0 to 32.0 cm) to 11.0 cm (23.0 to 34.0 cm). The mean length range within samples (7.3 cm, with a standard deviation of 1.81 cm) was slightly greater than that within samples from single-school summer catches in the North Atlantic Area (6.6 cm, with a standard deviation of 2.02 cm), but the difference between the means has no statistical significance.

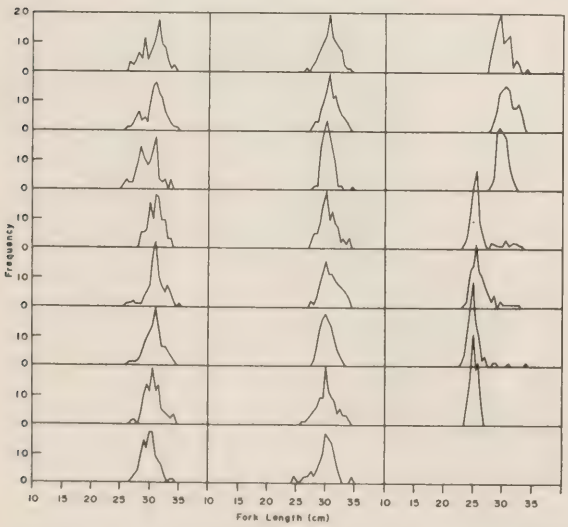

FIGURE 7.—Length-frequency distributions of Atlantic menhaden in samples from 23 single-set purse-seine catches from fall school-aggregations off Long Island, 1955-62.

The fall migratory school-aggregations off North Carolina consisted of length-groups represented farther northward during the summer, and individual aggregations contained fish of similar lengths. Fish lengths represented in samples from 41 single-set catches from these school-aggregations ranged from 8.5 to 35.0 cm (Figure 8). Because of selective fishing by the fleet on school-aggregations comprised of larger fish, the catch samples are accordingly weighted. The smallest length groups include young-of-the-year fish which had emigrated from estuarine nurseries at the end of the summer (June and Nicholson, 1964; Kroger, Dryfoos, and Huntsman, 1971). The most striking feature of the length-frequency curves is the relative homogeneity of fish lengths within individual school-aggregations, i.e., small fish are not represented in catch samples containing large fish, or vice versa. The least range in length within samples was 4.0 cm (9.0 to 13.0 cm) and the greatest 12.0 cm (22.0 to 34.0 and 22.5 to 34.5 cm). The mean of the range in length within samples was 8.4 cm, with a standard deviation of 6.13 cm. This was the largest mean difference and the greatest variation about the mean for any group of samples examined in this study. The length-frequency distributions of fish over about 25 cm were similar to those of single-school summer catches in the North Atlantic Area and to single-set catches from fall school-aggregations off Long Island (cf. Figure 7).

From an analysis of length and age data for 1955 to 1958, June and Nicholson (1964) postulated that these large school-aggregations that migrated southward along the North Carolina coast in November and December comprised portions, if not all, of the stocks which had spent the summer north of Cape Hatteras, N.C. More detailed analysis of the length-age data by Nicholson (1971a) and results of tagging studies

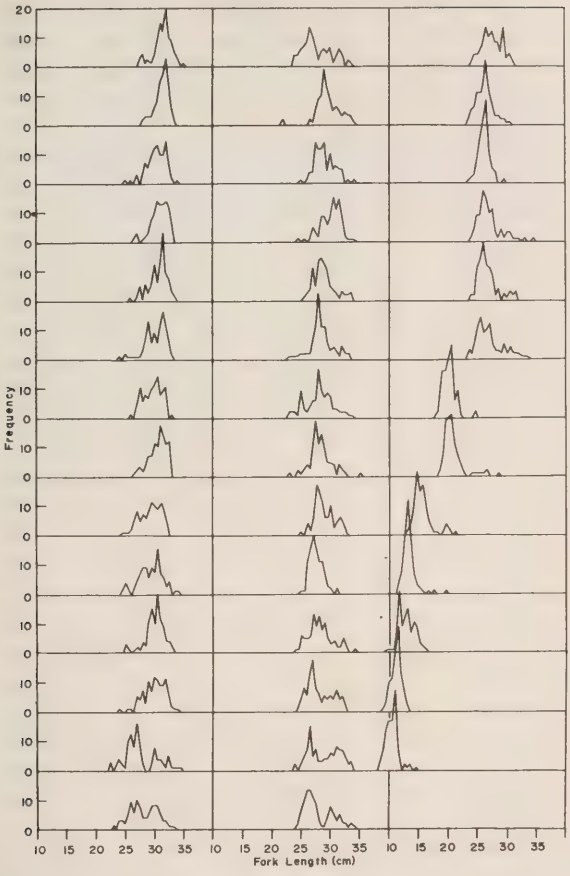

FIGURE 8.—Length-frequency distributions of Atlantic menhaden in samples from 41 single-set purse-seine catches from fall school-aggregations off North Carolina, 1955-62. The samples are arranged in order of decreasing fish length.

(Cheek et al., 1970) have confirmed and elaborated this hypothesis.

Briefly, the length-frequency data presented show a strong tendency for Atlantic menhaden to group by length. Summer schools are comprised of fish that are more nearly of the same length than is found among schools within any given area of the coast, or within the population as a whole, and there is an increase in the average length of fish within schools from south to north. Fall school-aggregations, which are usually fished only off Long Island and North Carolina, also consist of fish of similar lengths, but lengths within aggregations tend to be more variable than within summer schools.

SIZE OF SUMMER SCHOOLS IN RELATION TO FISH LENGTH

There was wide variation in the size (weight) of summer schools in relation to the average length of fish within a school. A plot of catch against mean length of fish in the 275 single-school catches (Figure 9) suggests a tendency for larger fish to occur in larger schools. The correlation between school size and mean fish length ($r = 0.144$) differs significantly from 0 ($P < 0.05$), and the relationship evidently is linear, since the arithmetic correlation coefficient is higher than that between log school size and log mean fish length ($r = 0.095$), or between log school size and mean fish length ($r = 0.103$). Comparison of the arithmetic correlation coefficients for the individual years, however, indicated heterogeneity ($\chi^2 = 17.14$; $P < 0.05$), so I plotted the data for each year separately and calculated trend lines (Figure 10). The occurrence of larger fish in larger schools is evident in some years, but in other years the trend was reversed, or there was no apparent relation between the two variables. Unequal representation of various length groups in different years may be responsible for the apparent heterogeneity of the data, but I conclude that annual

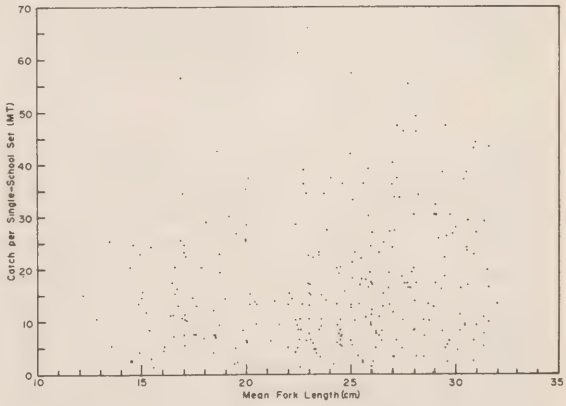

FIGURE 9.—Size of 275 single-school summer purse-seine catches of Atlantic menhaden plotted against the mean length of the fish in catch samples, 1955-62.

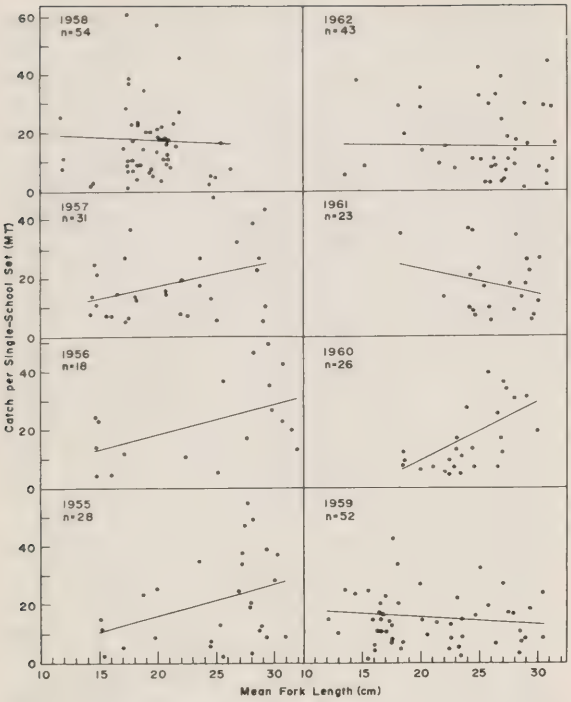

FIGURE 10.—Relationship between the size of single-school summer purse-seine catches of Atlantic menhaden and the mean length of fish in the catch sample, 1955-62.

differences in size of summer schools, which are independent of fish length, probably occur.

NUMBER OF FISH WITHIN SUMMER SCHOOLS IN RELATION TO FISH LENGTH

The number of fish within a school varied widely but, on the average, decreased as fish length increased. A plot of the estimated number of fish on the mean length of fish within the 275 single-school summer catches (Figure 11) indicates an inverse relationship between the two variables. The trend appears curvilinear; however, there is little difference among the correlation coefficients between the numbers of fish and their mean length ($r = -0.599$), between log number and mean fish length ($r = -0.597$), or between log number and log mean fish length ($r = -0.585$); all coefficients differ significantly from 0. The estimated number of fish within schools ranged from 500 (mean fish length 28.9 cm) to 655,400 (mean fish length 16.8 cm), with a mean of 86,776 fish.

In interpreting the above findings, it must be kept in mind that estimates of fish number are indirect and therefore subject to systematic bias. Furthermore, changes in the relation of school size (weight) and fish length between years were indicated in the previous section; therefore, a common regression equation may not be representative of actual changes in the numbers of fish of given size within schools. Accordingly, a trend line was not fitted to the data in Figure 11.

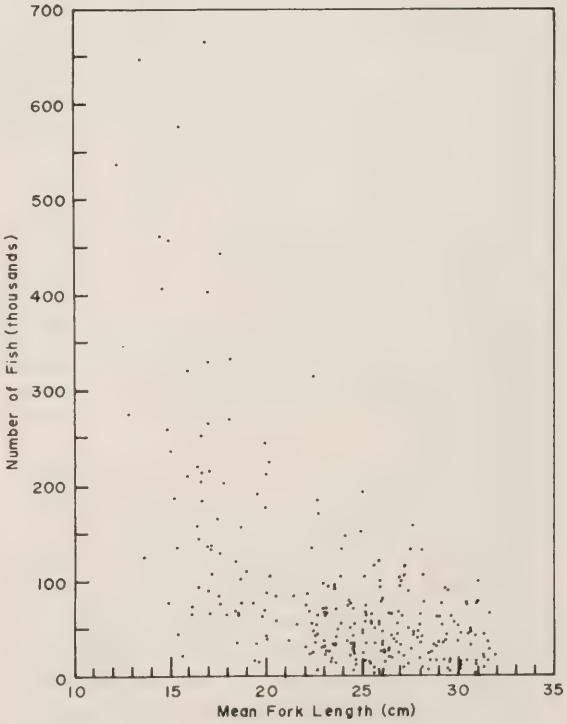

FIGURE 11.—Estimated number of Atlantic menhaden in 275 single-school summer purse-seine catches plotted against the mean length of fish in the catch sample, 1955-62.

SIZE OF SUMMER SCHOOLS IN RELATION TO APPARENT ABUNDANCE OF THE FISH

It was shown earlier that the mean single-school summer catch declined over the 8-year period in the two northern areas and fluctuated randomly in the two southern areas. To determine if these trends were an artifact of sampling or actually reflected variations in apparent abundance of the summer stock in the respective areas, I plotted the average catch per vessel week given by Nicholson (1971b) against the mean single-school summer catch in the corresponding season. There was good agreement between the two estimates in every area (Figure 12), but the relationship was closer for the South Atlantic and Middle Atlantic Areas than for the

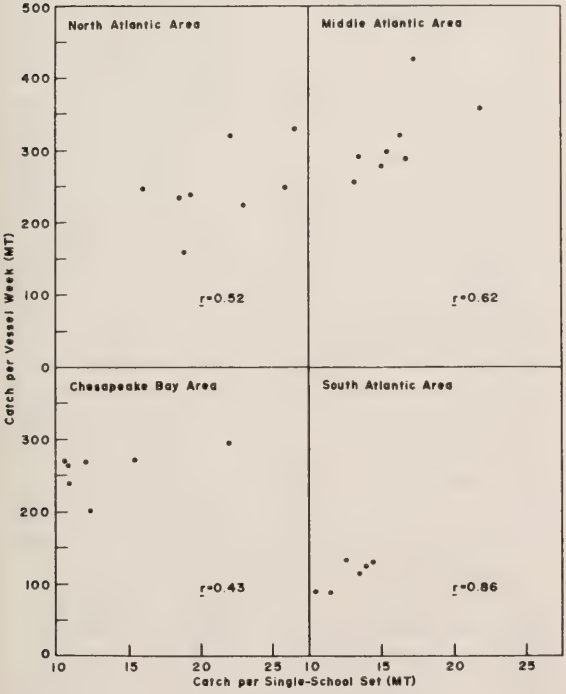

FIGURE 12.—Relationship between the purse-seine catch of Atlantic menhaden per vessel week and the mean single-school summer catch in the major statistical areas, 1955-62.

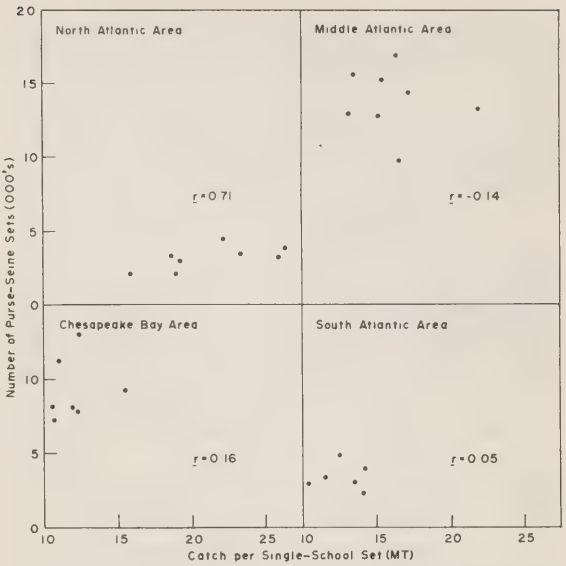

FIGURE 13.—Relationship between the estimated number of purse-seine sets for Atlantic menhaden and the mean single-school summer catch in the major statistical areas, 1955-62.

Chesapeake Bay and North Atlantic Areas. The correlation coefficient for the South Atlantic Area is significant at the 1% level and, that for the Middle Atlantic Area at the 5% level. Although the coefficients for the Chesapeake Bay and North Atlantic Areas are positive, neither differs significantly from 0. These findings indicate that summer schools became smaller as stock abundance in a given area decreased.

The relation between school number and school size is also of interest in assessing changes in stock abundance. A plot of the seasonal number of successful purse-seine sets (a measure of school density) given by Nicholson (1971b) on the corresponding mean single-school summer catch (Figure 13) shows a wide scattering of points within areas and considerable variability between areas. The correlation coefficient is positive for the Chesapeake Bay and North Atlantic Areas, negative for the Middle Atlantic Area, and about 0 for the South Atlantic Area, with only that for the North Atlantic Area having

borderline statistical significance ($P \sim 0.05$). If these results are real, it may be inferred from the positive correlations that larger schools were associated with greater school numbers. The negative correlation, on the other hand, suggests that schools tended to be more numerous as their average size decreased.

The reasons for the apparent discrepancies in the school density-size relationship in the different areas are not clear. The lack of any trend in the South Atlantic Area may result from variable availability of the schools. Fishermen and aircraft spotters report frequent disappearances of schools from surface coastal waters early in the day and occurrences of fish inside the extensive sounds that border the summer fishing grounds in this area (this behavior pattern of the fish may be associated with tidal currents passing through the numerous inlets and their relation to the abundant plankton food supply inside the sounds). A possible explanation for the inverse relationship between school size and number in the Middle Atlantic Area is that fishing captains tend to avoid the smaller fish and smaller schools when fish are abundant. Heavy fishing in the Middle Atlantic Area may also be a contributing factor in keeping the stock broken up into smaller schools. Fishing effort in this area averaged from 1½ to 4½ times greater than in any other area and increased by about 11% over the 8-year period (Nicholson, 1971b). There very likely is some level of fishing effort that disrupts the normal schooling habits of the fish, but the interrelationships involved appear to be much more complex than can be determined from the data in hand.

The main inference to be drawn from this section is that size of summer schools is related to stock abundance in each major fishing area. The school density-stock abundance relationship, however, needs to be clarified by analysis of data collected after 1962 when the catch dropped to the lowest levels since the 1930's.

DISCUSSION

Knowledge of the nature and consistency of groupings of Atlantic menhaden is fundamental to understanding the dynamics of the population. Results of this study demonstrated that the fishable stock occurs in schools or school-aggregations during most of the year. It is also known that the young fish school from the time of their entry into estuarine nurseries as larvae (June and Chamberlin, 1959; Reintjes and Pacheco, 1966). Thus, schooling is one of the basic behavior characteristics of this fish. June and Reintjes (1959) provided initial evidence that the fish school by size and to some extent by age and also showed that schools in a given locality more closely resemble each other in composition than schools from different localities. June and Nicholson (1964) and Nicholson (1971a) described in some detail the increase in average length and age of the fish with increased latitude and inferred annual north-south movements of the fish from seasonal changes in their length and age distributions. The findings of this paper support the conclusions of the foregoing studies and provide further insight into the variability of the distribution, composition, and size of summer schools and fall school-aggregations. But one of the critical unknowns is the extent to which such variability is related to stock density and, ultimately, to fishing.

Evidence presented here indicates that the size of summer schools is a function of stock abundance. It was also shown that an inverse relationship existed between fish length and size (weight) of summer schools. These findings suggest that there probably is an optimum school size for fish of given length that is most favorable for survival. If so, there must be a level below which the population must not be fished without running the risk of disrupting schooling to the point of inflicting irreparable damage to population resilience. While these hypotheses are unprovable with present data, the inference is that schooling marine fishes that are sought by surface sightings are more vulnerable from unregulated fishing than nonschooling species that are not subject to direct observation. Slight changes in the nature and consistency of grouping of Atlantic menhaden ought therefore to be considered in assessing both short- and long-term effects of fishing on the population.

The inverse relationship shown between fish length and the number of individuals within

summer schools also has important implications in regard to the yield that may be expected at different levels of fishing and to the well-being of the population. Since the fish are differentially distributed by length, with smaller fish occurring in the South Atlantic and Chesapeake Bay Areas during the greater part of the year, a disproportionate increase in the fraction of the population taken in these areas would be expected to result in a substantial reduction in the stock of larger fish available in the Middle and North Atlantic Areas. Putting it another way, a given unit of effort in the two southern areas imposes a higher fishing mortality rate. Moreover, immoderate fishing on the recruit stock in the two southern areas may also be expected to result in a drastic reduction in the size of the spawning stock. Thus, a stock-recruitment model that incorporates information on school size, number, and composition is less likely to fall short of realistic estimates of the levels of fishing commensurate with a desirable population structure and the optimum catches that may be expected therefrom.

If the role of schooling in the dynamics of the Atlantic menhaden population is to be understood, the research must be based on broader considerations than the classical methods of stock assessment. Limiting interpretation of changes in the population to simple relationships between fishing effort and catch is to ignore the dynamic aspects of fish schooling implied throughout this paper. Because of the selective nature of purse-seine fishing, fishermen's logbooks and catch records can only furnish indirect evidence of changes in the behavior and habits of the fish due to fishing. Furthermore, increased efficiency in the methods of menhaden fishing, coupled with technical improvements in fishing gear and vessels, has greatly altered long-term measures of effective fishing effort with the probable result that fishing mortality tends to be underestimated and changes in schooling of the fish minimized or perhaps obscured. Thus, there is a primary need for direct measures, independent of fishing, of school biomass and number and distribution of schools in the sea, including correlative measures of the fall school-aggregations off Long Island and North Carolina. With menhaden, direct aerial observations or photography and remote sensing are practicable (see, e.g., Roithmayr, 1970). Recent advances in underwater acoustical techniques (see, e.g., McClendon, 1968; Smith, 1970; Love, 1971) offer a supplementary means of identifying and quantitatively assessing the size and composition of menhaden schools.

Finally, development of a fully analytical approach to the role of schooling in the study of the dynamics of the Atlantic menhaden population requires a broad spectrum of information on the behavior of the fish in relation to environmental factors and other fishes. Briefly, what is needed is a more or less continuous picture of what the schools are doing. Included here are (1) the nature of short-term, i.e., day to day, changes in the behavior, structure, and distribution of summer schools in response to changes in light, salinity, temperature, currents, and food conditions, (2) the behavior of schools in isolation and in association with other fishes, (3) the primary mechanisms involved in the formation of school-aggregations and the seasonal migrations, and (4) the winter habits and whereabouts of the fish. There, for example, are no published data from which it is possible to estimate the swimming speed or endurance of which a school is capable in escaping a predator or a net. Much information can be provided from direct observations on the fish in free-swimming schools under a variety of life conditions. Aircraft are routinely employed in locating and directing fishing operations (Squire, 1961; June, 1963), yet little use has been made in menhaden research of either the information compiled by individual fish spotters or the facilities offered by the aircraft fleet. In practice this might simply require the recording of aerial observations during fishing operations and special reconnaissance flights as a means of assessing changes in the distribution and size of schools or school-aggregations during the fishing season, or mapping the migrations of this fish. Ancillary data on the behavior and physiology of the fish may be generated from experimental studies in aquaria, artificial ponds, and temporary enclosures in the sea. Any single approach to the study of schooling of Atlantic menhaden has

limitations, but a combination of methods, such as those outlined here, can lead to better understanding of the obligatory nature of schooling and its role in vital life processes of individuals and dynamics of the population.

EPILOGUE

This study was planned and most of the tabulations of data and writing completed before I left the Menhaden Program in 1964, but because of the press of other duties, I was unable to fulfill an obligation to finish the work earlier. My resolve to complete it at this time was renewed when I received Dr. Reuben Lasker's letter to former associates of Dr. Elton Sette soliciting papers to be included in this dedicatory issue of the *Fishery Bulletin*.

Some of the ideas contained in this study were inspired by Dr. Sette's papers dealing with the Atlantic mackerel and the Pacific sardine and from my discussions with him of apparent similarities in the behavior and biology of the Atlantic menhaden and the Pacific sardine. It indeed is a privilege for me to acknowledge, in this place, my appreciation of Elton's influence on my concept of the disicplines of fishery biology, his sharing of an interest and enthusiasm for tropical botany and color photography, and lastly his challenging opposition on the tennis court.

ACKNOWLEDGMENT

I wish to thank Mary K. Hancock, who compiled the menhaden vessel logbook records and assisted in processing the basic catch-sample data used in this study.

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ACTIVITY OF HAWAIIAN REEF FISHES DURING THE EVENING AND MORNING TRANSITIONS BETWEEN DAYLIGHT AND DARKNESS

EDMUND S. HOBSON[1]

ABSTRACT

Activity during the morning and evening transitions between day and night was studied as part of a broad investigation of ecological relations among reef fishes in Kona, Hawaii, during 1969 and 1970.

Most of the fishes are either diurnal or nocturnal, the former being mainly inactive at night, the latter mainly inactive in daylight. During active periods their behavior is dominated by feeding, whereas inactive periods are dominated by measures to enhance security. Thus twilight behavior involves primarily a changeover from feeding to sheltering, and the reverse. Migrations of various types between shelter locations, where they rest, and feeding grounds are a major element of the transition periods.

The transition events proceed in an established, well-defined sequence. In the evening, after the diurnal fishes have descended to shelter and before the nocturnal fishes have risen into the water column, there is an interim period of about 20 min during which both diurnal and nocturnal fishes are close to the substrate; it is at this time that reef fishes are most vulnerable to predators, and the proximity of cover offers protection. Similar behavior occurs among related fishes in the Gulf of California. The interim period in Kona corresponds in time relative to sunrise and sunset to the period during which schooling fishes in the Gulf of California are under heaviest attack; however, because schooling fishes and the predators that exploit them are not major elements of the Kona fauna, overt predator-prey interactions are not prominent there. Thus the well-ordered pattern of events that characterizes twilight in Kona also occurs on other reefs widespread in tropical seas, whether or not there exists in each of these areas today a severe threat from large piscivorous predators. The twilight pattern of actions is the result of a long evolution that in any one area transcends the existing situation and species. Because predator-prey interactions among fishes have been influenced throughout time by certain basic and unchanging phenomena, the similarity of twilight activity patterns among fishes on widely separated reefs today reflects the impact of a historic threat from predators.

Most fishes on tropical reefs are active either by day or by night, with the diurnal species mostly inactive in darkness and the nocturnal species mostly inactive in daylight (Hobson, 1965, 1968; Starck and Davis, 1966). The changeover from one situation to the other is a complex process, with events following a well-defined sequence. This report describes the significant events during the evening and morning transition periods in Kona, Hawaii, between June 1969 and August 1970. It is a segment of a broad study of ecological relations among Hawaiian reef fishes. The present report, which deals with the twilight situation, will be followed by a second report covering the situations throughout day and night, respectively, and including a detailed analysis of food habits (Hobson, in preparation). Some highlights of this program were outlined earlier (Hobson, 1970).

METHODS

This study is based on observations that spanned evening twilight on 20 occasions and

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morning twilight on 18 occasions. Generally over 2 hr were spent on station during each observation period, although the transition events detailed in this report were concentrated into a span of about 1 hr, as discussed below. Before the data presented in this report were collected, general observations in the study area at these times of day had provided a broad understanding of the twilight transition. Also contributing significantly to this understanding were extensive observations made during twilight in other seas, especially in the Gulf of California (Hobson, 1965, 1968), where related fishes have similar behavior. With this background and using scuba, I was able to recognize and record what I knew to be significant events and to note the time and other associated characteristics. Additionally, some data from observations made at various times of day and night during other segments of the program in Kona are pertinent to the present report and thus used here. Furthermore, interpretation of the twilight activities benefited significantly from these other phases of the overall Kona program.

Throughout all twilight observation periods, Lloyd D. Richards, stationed on the sea floor nearby, recorded incident light in foot-candles each minute with a photometer facing the water's surface. In this report, all records of light levels during specific events refer to these readings. To minimize instrument error, two photometers of the same model (Weston Ranger 9, universal exposure meter, Model 348)[2] were alternated. The accuracy of the absolute values obtained with these inexpensive instruments is not considered critical; rather, the primary concern is that the relative values are consistent, thus permitting comparisons of behavior relative to time and light between one observation period and another.

The time of specific events are presented relative to time of sunrise or sunset, as calculated for the longitude and latitude of the study area using the Nautical Almanac, U.S. Naval Observatory. An event occurring at about the same time each day relative to sunrise or sunset, will, in time of day, vary by as much as several hours over the course of the year. This fact reduced any bias that might have resulted from subconsciously looking for an event at a specific time. Although I was alert for certain events in sequence, based on familiarity with the general situation, I consciously avoided thinking in terms of time relative to sunrise or sunset during the observations. This was not difficult to do. I did not calculate time of sunrise or sunset until after a period of observation, and neither could have been directly observed, even had I not been underwater at the time; in the study area a large volcano blocks much of the eastern sky, and the western sky generally is obscured by clouds at the end of the day. Furthermore, usually a week or more elapsed between observations of morning or evening twilight, so that the time of sunrise and sunset changed substantially from one set of observations to the next. Finally, I did not translate the data from time of day to time relative to sunrise or sunset until the program in Hawaii was completed.

Obviously all events judged significant were not witnessed during each observation period. Many were evident only in certain locations, and several occurred at about the same time. Consequently, the number of times that data were recorded for each event varies widely.

Names used for the fishes generally follow those given by Gosline and Brock (1960); exceptions occur where more recent taxonomic studies have indicated changes. Most of the fishes are referred to some broad feeding category, such as being a herbivore, a plankton feeder, etc. These general designations are based on detailed study of food habits to be reported elsewhere (Hobson, in preparation).

In parentheses following the first mention of each fish species are given a mean and range of standard lengths, for example (235: 173-284 mm). These figures represent the sizes of specimens of that species that were collected for the food habit analysis (Hobson, in preparation). In collecting these specimens an attempt was made to sample individuals of sizes that showed behavior of adults. Hence these figures provide a good measure of the relative sizes of

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

the different species, as relating to the activity described in the present report. This information is important because the size of a given fish is reflected in its behavior during twilight, as discussed below.

A number of species prominent on Hawaiian reefs are not mentioned in this report. My coverage is confined to species in which I recognized behavior relating specifically to the twilight transition period on the three reefs where twilight behavior was studied. Some other species not prominent on these reefs are abundant elsewhere and were studied during other phases of the overall project. These other segments of the work in Kona yielded no data inconsistent with what is reported or discussed below.

STUDY LOCATIONS

The reef habitat on the Kona coast is restricted to a narrow shelf close to shore. From the base of a rough, basalt shore cliff, the sea floor in most locations slopes gently downward for distances of between 50 and 600 m from shore. At this point, where the water is generally about 20 to 25 m deep, the bottom drops abruptly to great depths.

Most of the data for this report were collected from three inshore locations, all at depths between 5 and 10 m. Each location has a distinctly different substrate. Station 1 is in Kealakekua Bay among massive heads of the coral *Porites pukoensis* rising 2 to 3 m above the sea floor. Station 2 is in Honaunau Bay among an extensive field of the coral *Porites compressus* growing in fingerlike branches 10 to 15 mm wide. Station 3 is also in Honaunau Bay, but among massive basalt boulders 2 to 3 m across that are largely overgrown with encrusting algae and corals. These boulders are variably interspersed with the forms of both *P. pukoensis* and *P. compressus* described above.

The remarkably constant weather and water conditions that characterize the Kona coast held true throughout the 15 months of observations. Consequently, variables inherent in changing environmental conditions were minimized, making it easier to recognize activity patterns associated with the twilight transition periods.

TRANSITION FROM DAY TO NIGHT

It is difficult to determine exactly when the daytime situation begins to move toward that prevailing after dark. In large part, this difficulty reflects variations in activity of many diurnal fishes because of differing water transparencies, and even more when variable cloud cover causes light levels to fluctuate. These variations are difficult to distinguish from those associated with the lesser light levels of the advancing afternoon. Additionally, as the day progresses, activity of diurnal fishes changes subtly in many other ways that may or may not relate to a transition to the nocturnal mode. The situation prevailing throughout the day (Figure 1), including variations with changing light levels and other factors, is described elsewhere (Hobson, in preparation). This report is concerned with the more striking transformations that occur during the transition between daylight and darkness, beginning about 15 min before sunset and lasting until about 45 min after sunset—a span of about 1 hr. Three major periods are readily recognized: 1) the cover-seeking of the diurnal fishes; 2) an interim period; and 3) the mass emergence of nocturnal species.

COVER-SEEKING OF THE DIURNAL FISHES

Initial Overt Phase of the Transition

An early cue to the developing transition lies with the plankton-feeding fishes that swim during the day in stationary aggregations up in the water column. Prominent among these are the damselfishes *Abudefduf abdominalis* (142: 105-162 mm), *Chromis leucurus* (57: 37-70 mm), *C. ovalis* (124: 121-138 mm), *C. vanderbilti* (38: 17-46 mm), and *Dascyllus albisella* (79: 42-95 mm). The distance of each fish from the substrate is related to its size, because the larger individuals swim at higher levels in the water column. These fishes descend progressively closer to the sea floor as light diminishes. Members of the smallest species, *Chromis vanderbilti*, are the first to take cover; they seldom move more than a meter above the reef on even the

FIGURE 1.—Daytime on a coral reef in Kona, Hawaii. Most of the fishes are acanthurids, including *Ctenochaetus strigosus*, *Acanthurus leucopareius*, and *Zebrasoma flavescens*. Other fishes include *Centropyge potteri* and *Zanclus canescens*.

brightest days, and by 15 min before sunset all of them have dispersed among holes in the reef. The progressive descent of the other plankton-feeding damselfishes is treated below.

As individuals of *C. vanderbilti* are taking shelter, the transition to the nocturnal situation is clearly underway. The numbers of smaller wrasses active on the reef have been noticeably declining since at least 30 min before sunset, though many still remain in view. More obvious, an increased tendency to aggregate is exhibited by some of the smaller herbivorous fishes, including the surgeonfishes *Acanthurus nigrofuscus* (120: 100-140 mm) and *Ctenochaetus strigosus* (125: 110-145 mm) and also the parrotfish *Scarus taeniurus* (210: 180-243 mm). These aggregations continue to develop through sunset and into early twilight.

By about 5 min after sunset the last individuals of many diurnal species have taken cover, including the last of the smaller wrasses. No data are available on precisely when the larger wrasses seek cover (those exceeding a length of about 350 mm are uncommon in the study areas). Nevertheless, my observations agree with those of Gosline and Brock (1960), who stated that all Hawaiian labrids are inactive at night.

Two species of smaller labrids are representative: *Thalassoma duperrey* (125: 103-146 mm) and *Labroides phthirophagus* (63: 33-91 mm). (I did not collect specimens of the latter species —size data are from Youngbluth, 1968.) *T. duperrey* probably is the most numerous of the readily observed species of fish overall in the various Hawaiian reef habitats and thus serves well as an indicator species. *L. phthirophagus* is not abundant, but as a cleaner fish that centers its activity around well-defined stations (Randall, 1958; Youngbluth, 1968), individuals can be readily recognized from one evening to another.

Observations on Thalassoma duperrey.—On five occasions I was confident that I observed

the last individual of *T. duperrey* active in my immediate area take shelter (Figure 2). Each of these individuals swam in and out of coral crevices several times before finally slipping into a hole where it remained. On subsequent close inspection I found each one lying on its side in the hole, and intermittent checks over the next hour disclosed each still in the same position. Following one such observation, a predawn inspection the next morning found the fish in the same spot.

There is evidence that, on a given evening, an individual is intent on resting in a particular spot. Two incidental observations give credence to this view. One evening I lay prone and immobile across a large coral head (*Porites*), watching the many *T. duperrey* around me, and waiting to note the last one that took cover. The behavior of one individual was unusual: it circled close by regarding me more intensely than seemed normal, then swam away. Several times this same fish reappeared, repeated this behavior, then swam away again. Curious, I abandoned my position and followed when the fish reappeared. After being led in a circle, I found myself back at the original location, where the fish slipped into a coral crevice in the spot where I had been lying. Only then did it occur to me that this fish had behaved abnormally probably because I had been blocking entry to its nocturnal resting spot. Other individuals of *T. duperrey* were still active in the area when this incident occurred, making it uncertain whether the fish actually had been delayed in attaining cover. A similar incident later was more conclusive. Again, I rested motionless, watching the many individuals of this labrid during the evening transition period, this time leaning against a vertical wall of coral (*Porites*). One individual swam close by, then moved to a low ledge about 2 m away, where it then swam back and forth, watching me continuously. Several times it momentarily left the ledge, approached me, and then darted back to the ledge. Recalling the earlier incident, I did not move from my station until long after all other fish of this species had gone under cover. Finally, 12 min after sunset (light 0.8 ft-c), with the behavior of the labrid under observation still unchanged, I moved away. Immediately, it swam to my former location and slipped into a crevice. Later, using a light, I could see this wrasse lying on its side, wedged back in the crevice. (These two incidents are not included among the data represented in Figure 2, which includes only situations judged normal.)

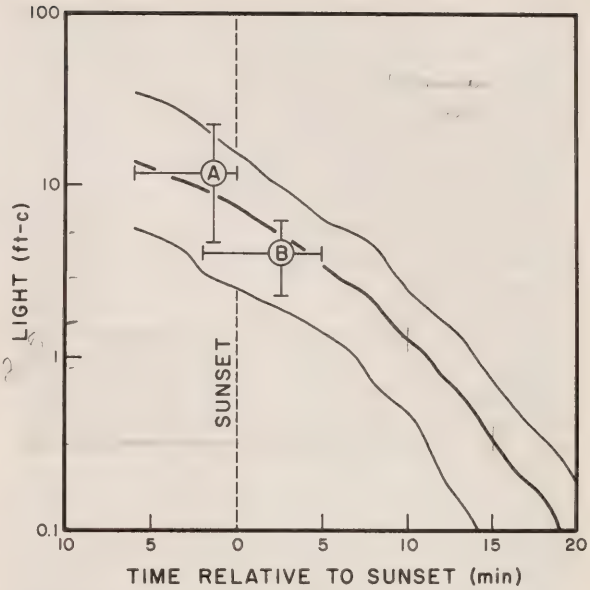

FIGURE 2.—Some characteristics of certain labrids during evening twilight. Each lettered symbol represents a species: A. *Thalassoma duperrey*—when the last individual took cover on five evenings. B. *Labroides phthirophagus*—when one individual took cover on five evenings. The circle represents mean values of both time and incident light when the event occurred; the vertical line, the range of incident light values; and the horizontal line, the range in time relative to sunset. The three diagonal lines represent: the maximum light values for each minute relative to sunset during all evening twilight observation periods (top line), the minimum values for each minute (bottom line), and the mean values (heavy median line).

These observations indicate that a fish can have a strong affinity for a specific resting spot. However, I have no evidence that this is more than a short-term phenomenon. Many nocturnal resting spots of *T. duperrey*, and other fishes, were discovered incidentally during other phases of the work in Kona when I closely inspected crevices in the coral during the night. When circumstances permitted, followup observations

were made at various times during subsequent nights. Although a given resting spot was frequently occupied over several nights by what seemed to be the same fish, this did not hold true for longer than a week or so. I doubt that my repeated intrusions disturbed these fishes sufficiently to influence a change of location. Usually a spot occupied by a resting fish on one evening was vacant when next observed on a subsequent night.

Observations on Labroides phthirophagus.—Individuals of this species, like other labrids, seek cover for the evening during the period from immediately before to just after sunset. *L. phthirophagus*, like *T. duperrey*, finds nocturnal shelter in crevices of rock or coral. But with this species, unlike the others, individuals can readily be recognized from one day to the next, owing to their close association with well-defined cleaning stations. Thus, whereas observations of *T. duperrey* each evening involved only the last active member of the species, the cover-seeking of one particular individual *L. phthirophagus* was timed over five different evenings (Figure 2). The one instance when this fish took shelter 5 min after sunset was the latest that any of the smaller labrids were seen active.

L. phthirophagus cleans other fishes at its station until it takes shelter. Frequently other species still hover at the station in soliciting fashion (see Losey, 1971) after the resident cleaner has retired for the night.

Twilight Upsurge in Activity

Visible activity among many diurnal fishes rises sharply at about the time of sunset. However, feeding generally is not involved; rather, the upsurge stems mostly from the many species on the reef that migrate from one location to another at this time, and also to increased interspecific and intraspecific aggression, at least much of which is related to territoriality. In addition, some species show at this time an increased tendency to aggregate and to swim in more visible locations.

Above, I note that prior to sunset some of the smaller herbivores increasingly aggregate a meter or so above the reef. Beginning with this event, the phenomenon gains momentum, encompassing more and larger fishes, especially among the surgeonfishes and parrotfishes. By 5 min after sunset this activity has reached its maximum level, even though most of the smaller species among which it first appeared by then have discontinued the activity and have settled under cover.

There seem to be two major types of aggregations: Assemblages of one type, often of mixed species, mill about 1 or 2 m above certain parts of the reef; and assemblages of the other type, mostly of a single species, move with seeming purpose from one location on the reef to another. Each of these types of assemblages is treated separately below.

The milling assemblages.—During about a 10-min period, 5 to 15 min after sunset, the scene on many parts of the reef is dominated by large, essentially stationary, mixed-species aggregations that mill about in certain locations 1 or 2 m above the substrate. Various surgeonfishes predominate, especially *Zebrasoma flavescens* (163: 130-195 mm), *Acanthurus achilles* (182: 165-200 mm), *A. nigroris* (165: 130-180 mm), *A. leucopareius* (190: 185-210 mm), and *Naso lituratus* (180: 156-220 mm). Also prominent are the parrotfish *Scarus sordidus* (230: 205-260 mm), the triggerfishes *Melichthys niger* (165: 122-195 mm), and the filefish *Cantherines dumerili* (200: 171-240 mm).

The twilight migrations.—Some members of many species migrate at this time from one location on the reef to another. Although the patterns remain obscure, this activity involves movements that occur consistently in certain locations. Evening after evening specific routes are followed, in which certain species stream continuously past a given point in long drawn-out processions over a period of several minutes.

Prominent participants include members of certain species, including the surgeonfish *Naso hexacanthus* (261: 202-392 mm) and the damselfish *Chromis verater* (120: 100-141 mm), that feed on plankton during the day high in the

water column at the outer edge of the reef. Many of these fishes show a migratory pattern up into the shallower parts of the reef at nightfall, but the pattern is obscured by the circumstance that other individuals of these same species do not move inshore, but instead remain throughout the night at the outer edge of the reef, nestled among the coral on the sea floor below their midwater feeding areas.

Many of the smaller herbivores, including the surgeonfishes *Zebrasoma flavescens* and *Ctenochaetus strigosus*, as well as the parrotfish *Scarus sordidus*, exhibit similar movements. These patterns are obscured because on any given night relatively few individuals of these species join such migrations; many others of the same species do not, including some that are prominent in the milling assemblages noted above. It remains unknown just what sort of redistribution pattern is achieved by these movements.

Descent of the Plankton-Feeding Damselfishes

Individuals of the smallest plankton-feeding damselfish *Chromis vanderbilti* have scattered among the rocks by about 15 min before sunset, as noted above. During the few minutes immediately following sunset, members of the next smallest species, *C. leucurus*, settle individually in coral crevices. On three evenings the time and light levels were recorded as the last individual of *C. leucurus* in my surroundings took shelter (Figure 3).

The larger species, including *Abudefduf abdominalis*, *Chromis ovalis*, *C. verater*, and *Dascyllus albisella*, continue to drop lower in the water column throughout this period. Precise times for the different stages of the descent are not available, but all drop at a similar rate, a fact probably related to their similar sizes. The descent begins well before sunset, when individuals in 8 m of water, for example, are about 5 m over the sea floor. At 8 to 10 min after sunset they are about 1 to 2 m over the coral, and here contribute to the general activity, where the milling aggregations and migrating schools, described above, dominate the scene.

Vacating the Water Column

Throughout the time that the milling aggregations and migrating schools swim over the reef, individuals from these assemblages are descending to cover below. Nevertheless, a substantial number still swim in the water above the reef, along with the small groups of larger plankton-feeding damselfishes, at about 10 to 15 min after sunset. Then, abruptly, the vast majority of these fishes suddenly drop to the reef below, leaving the water column essentially deserted. This is a well-defined phenomenon, and on 12 evenings the time and light were recorded when it occurred (Figure 3).

Cover-Seeking of Other Diurnal Fishes

Also going under cover at about the time that the water column is vacated are the larger parrotfishes *Scarus rubroviolaceus* (366: 267-475 mm) and *S. perspicillatus* (348: 269-463 mm).

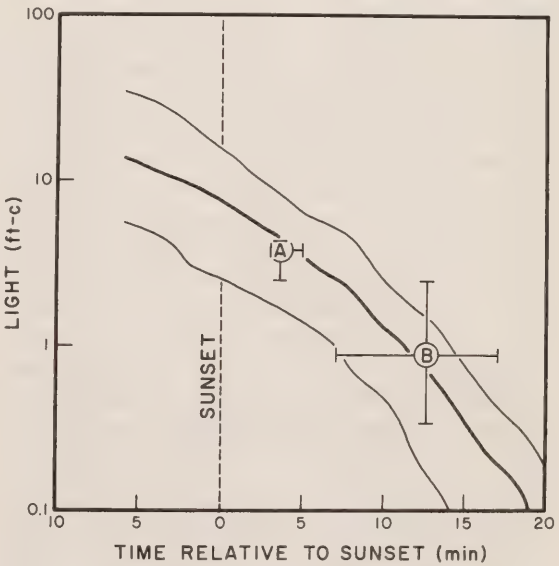

FIGURE 3.—Some characteristics of certain diurnal fishes during evening twilight. A. *Chromis leucurus*: when the last individual took cover on three evenings. B. When the water column was abruptly vacated by diurnal fishes on 12 evenings. For explanation of symbols, see legend for Figure 2.

The smaller parrotfishes had sought shelter earlier. Gone now too are the triggerfishes *Sufflamen bursa* (140: 109-164 mm) and *Rhinecanthus rectangulus* (142: 114-170 mm), as well as the filefishes *Pervagor spilosoma* (85: 64-120 mm) and *Cantherines sandwichiensis* (116: 84-132 mm), all of which had remained close to the substrate throughout their active periods during daylight and early twilight. Because most of these and many other diurnal species are not especially numerous on all of the study areas, often none are in view for long periods even during those times of day when they are most active; therefore, it would not have been meaningful to record the last individual of each species that was seen to take cover, as was done with the ubiquitous *Thalassoma duperrey* and a few other species treated in this report. This procedure is meaningful only with species whose members are so numerous and widespread that in all study areas some of them are always in view during their active periods. Nevertheless, these species, as described above, are only rarely seen in exposed positions after the water column has been vacated.

Many sedentary diurnal fishes find shelter during this period too. One suddenly realizes that such species as the hawkfishes *Paracirrhites forsteri* (139: 93-181 mm), *P. arcatus* (82: 49-101 mm), and *Cirrhitops fasciatus* (76: 39-91 mm) are only occasionally visible in locations where they are numerous during daylight. The same is true of the blennies *Exallias brevis* (94: 70-106 mm) and *Cirripectus variolosus* (73: 66-80 mm). Relative activity in species that are at least overtly inactive is difficult to quantify. Nevertheless, after the nocturnal situation prevails, about 30 min after the free-swimming fishes vacate the water column, these sedentary diurnal fishes rarely occur in exposed positions.

THE EVENING INTERIM PERIOD

When the last of those diurnal fishes swimming above the coral abruptly descend to the ocean floor, about 10 to 15 min after sunset, the evening interim period begins. At the outset, many diurnal fishes still mill about in pockets among the coral, close to the substrate. Prominent among these are the medium-sized surgeonfishes, such as *Acanthurus achilles*, that were prominent in the milling aggregations earlier. In addition, a few of the larger surgeonfishes, like *A. dussumieri* (340: 302-390 mm), still swim slowly over the coral in small scattered schools, but these do not diminish the prevailing quiescence. The closely related moorish idol, *Zanclus canescens* (108: 74-137 mm), still swims in groups of three or four, but close to the substrate. The butterfishes, family Chaetodontidae, often remain paired, as during midday, but some already show colorations that are different from those seen in daylight; these include *Chaetodon auriga* (151: 132-160 mm), *C. ornatissimus* (119: 95-140 mm), *C. multicinctus* (84: 78-94 mm), and *C. unimaculatus* (85: 66-102 mm), which become progressively less active and stay close to the coral. Damselfishes too, including *Pomacentrus jenkinsi* (89: 80-100 mm), and *Plectroglyphidodon johnstonianus* (60: 39-70 mm), though generally solitary, remain active close to coral and rock shelter at this time. The chaetodontid *Centropyge potteri* (80: 69-86 mm) behaves much like these damselfishes.

Into this situation of rapidly diminishing activity among diurnal species, the nocturnal species begin to emerge from the caves and crevices of the reef, in which they have passed the daytime. The first to appear is the cardinalfish *Apogon snyderi* (96: 82-130 mm), which remains close to the substrate, frequently mixing with the diurnal species that are settling there. A second cardinalfish, *A. menesemus* (114: 90-134 mm), soon follows its congener into the open. The initial sightings of *A. snyderi* and *A. menesemus* moving away from shelter were recorded on four and five evenings, respectively (Figure 4).

Several minutes later, when the diurnal species still in view are becoming more and more quiescent, the first of the squirrelfishes, the relatively large *Holocentrus sammara* (162: 128-202 mm), appears. This event was recorded on four evenings (Figure 5). Throughout the day, some individuals of both *A. snyderi* and *H. sammara* hover in view at the entrances to their diurnal retreats; consequently, one must be thoroughly familiar with these fishes to recognize

the subtle behavioral distinctions that characterize their initial moves away from shelter in the evening.

The interim is aptly termed the "quiet period," because so little activity is visible to an observer. The small fishes, both diurnal and nocturnal, are close to the sheltering substrate at this time. The term "quiet," as used here, refers to an absence of observable activity, not to an absence of sound. In fact, vocalizing of many animals increases throughout the transition period (see, for example, Cummings, Brahy, and Herrnkind, 1964).

During the latter part of the interim, or quiet, period, a few individuals of *Myripristis* spp. move out of their caves but stay close to the substrate. When the members of these species suddenly boil out of their caves 30 to 35 min after sunset, this striking event marks an abrupt end to the evening interim period.

THE MASS EMERGENCE OF NOCTURNAL FISHES

Reoccupation of the Water Column

The darkening water column suddenly becomes reoccupied by a horde of fishes when squirrelfishes of the genus *Myripristis* come streaming out of their diurnal retreats. The timing of this spectacular event was recorded on eight different evenings (Figure 5). Three species prominent on the study reefs, *Myripristis argyromus* (176: 116-210 mm), *M. multiradiatus*

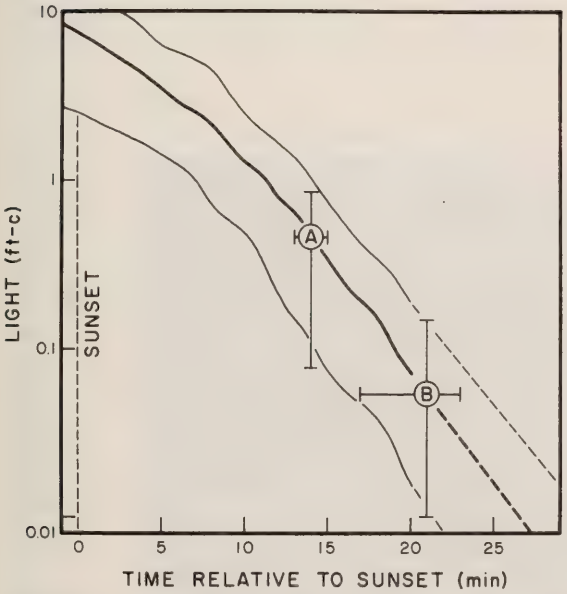

FIGURE 4.—Some characteristics of certain apogonids during evening twilight. A. *Apogon snyderi*: when the first individual left cover on four evenings. B. *Apogon menesemus*: when the first individual left cover on five evenings. For explanation of symbols, see legend for Figure 2. In addition, the broken diagonal lines represent estimated light values. Because of instrument limitations, light readings later than about 20 min after sunset were often unreliable, and therefore values beyond this point were estimated by projecting the established lines.

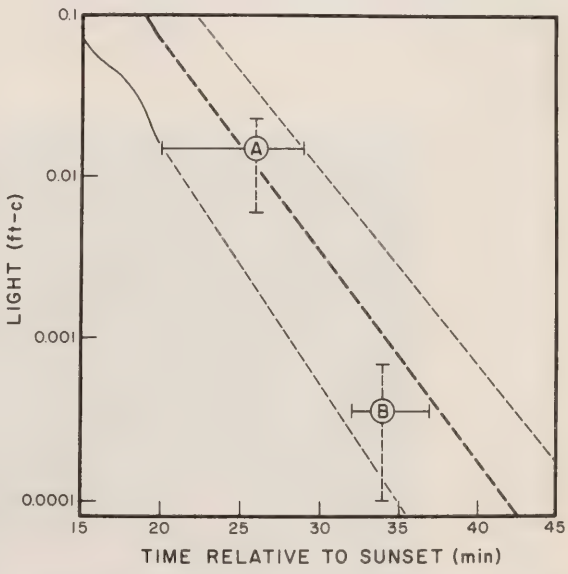

FIGURE 5.—Some characteristics of certain holocentrids during evening twilight. A. *Holocentrus sammara*: when the first individual left cover on four evenings. B. *Myripristis* spp: when large numbers of these fishes abruptly appeared in the water column on eight evenings. For explanation of symbols, see legends for Figures 2 and 4. In addition, broken lines representing range of light values in species symbols indicate that these were estimated for each observation by projecting the established line beyond 20 min after sunset.

(120: 74-145 mm), and *M. berndti* (169: 136-270 mm), all emerge at the same time. All move right up into the water column, although *M. multiradiatus*, the smallest of the three, stays closer to the reef than the other two. Almost immediately, many individuals of *M. argyromus* and *M. berndti* move offshore in mass. That fishes of this genus migrate offshore at night was noted by Gosline (1965), and their nocturnal plankton-feeding habits have been established (Hobson, in preparation).

At about the same time, bigeyes, *Priacanthus cruentatus* (173: 115-255 mm), rise from the rock and coral crevices that had sheltered them in daylight and, forming schools high above the reef, most of them swim offshore. The offshore migration at night by *P. cruentatus* was noted by Gosline (1965), and the feeding habits of this fish were studied (Hobson, in preparation).

At about the same time that fishes are reoccupying the water column, many other nocturnal fishes that are active only close to the substrate begin to be seen for the first time. These are mostly small species under about 200 mm long, and all are predators. Included are a number of squirrelfishes of the genus *Holocentrus*, including *H. xantherythrus* (106: 88-123 mm), *H. diadema* (109: 85-127 mm), *H. lacteoguttatus* (88: 52-104 mm), *H. tiere* (141: 67-235 mm), and *Holotrachys lima* (91: 70-113 mm); also the scorpionfishes *Dendrochirus brachypterus* (99: 80-118 mm), *Pterois sphex* (83: 58-121 mm), and *Scorpaena coniorta* (46: 26-67 mm), and the brotulid *Brotula multibarbata* (169: 73-250 mm). The nocturnal feeding habits of these fishes were studied (Hobson, in preparation).

To the human eye, it is nighttime on the reef at about 50 min after sunset, although the last vestige of daylight is still visible on the water's surface overhead. By this time the nocturnal situation prevails and will continue to do so until morning (Figure 6).

FIGURE 6.—Nightime on a coral reef in Kona, Hawaii. The fishes swimming above the reef are squirrelfish, *Myripristis* spp. At lower right center a single surgeonfish, *Zebrasoma flavenscens*, is nestled among the coral; the horizontal white bar on its side is, in adults, a feature of its nocturnal coloration.

TRANSITION FROM NIGHT TO DAY

As is true of the transition from day to night, it is difficult to determine exactly when the nighttime situation begins to give away to that prevailing during daylight. In large part, this difficulty reflects the great variation in activity among fishes at night relative to the amount of moonlight. The situation throughout the night, including variations under different levels of moonlight, is described elsewhere (Hobson, in preparation). This report is concerned with the more striking transformations that occur during the transition from darkness to daylight, beginning about 45 min before sunrise and lasting until about 15 min after sunrise—a total of about 1 hr. As is true of the evening transition, described above, three major periods are readily recognized: 1) the cover-seeking of the nocturnal fishes; 2) the morning interim period; and 3) the mass emergence of diurnal species.

COVER-SEEKING OF THE NOCTURNAL FISHES

Return of the Offshore Feeders

When there is no moonlight, an underwater observer notices the first trace of sunlight on the waters surface overhead about 1 hr before sunrise. Nevertheless, not for another 10 to 15 min do the fishes display overt signs that the transition to their daytime behavior is underway. Then, about 40 to 50 min before sunrise, the numbers of *Myripristis* spp. and *Priacanthus cruentatus* increase sharply near the caves where they pass the daylight hours. To some extent this is the assembling here of those individuals that had remained on the reef during the night, but mostly this marks the return to the reef of individuals that had migrated elsewhere.

The species of *Myripristis* become simultaneously so abundant everywhere that it is uncertain to what extent they have arrived together in schools or have converged simultaneously as solitary individuals onto the reef. The behavior of *P. cruentatus* is clearer. Being far less abundant than *Myripristis*, individuals of *P. cruentatus* are seen arriving in discrete schools, swimming high above the reef. These schools were especially apparent when an arrival point for the species was discovered at Honaunau, at a location near a coral cave midway down a steep slope. The crest of the slope is in water 12 m deep, the base is about 35 m deep, and the cave is at a depth of about 20 m. On six mornings, I witnessed the arrival here of a large school of *P. cruentatus* (Figure 7). Although a few early arrivals had already been in the area for as long as 10 min, the sudden appearance of the school, containing 30 to 50 fish, was a readily recognized event. After arriving together, many of these fish remained as a unit, milling close to the substrate just outside the entrance to the cave; however, many others of the group dispersed along the face of the slope, where much cover is available under overhanging coral growths. After about 10 min, during which these fish hovered close to the coral, all gradually took shelter: the majority entered the cave, whereas others, either as individuals or groups of a few fish, found cover in the varied crevices and smaller caves along the face of the slope. On the two occasions when the time was noted, the last of these fish were seen entering shelter at 29 and 32 min before sunrise, respectively.

After the initial upsurge in their numbers on the reef, some *Myripristis* go under cover right away, but most continue to swim above the coral for 10 min or so. On eight mornings I noted when the last of these had entered their caves (Figure 7).

Cover-Seeking of Other Nocturnal Fishes

About the time that *Priacanthus cruentatus* and *Myripristis* spp. are reappearing on the reef in large numbers, members of at least most of the other, less conspicuous nocturnal species are still active close to the substrate. It remains uncertain just when, in response to the approaching dawn, many nocturnal fishes cease to range into exposed positions. *Holotrachys lima, Dendrochirus brachypterus, Pterois sphex, Scorpaena coniorta, Brotula multibarbata,* and others are among the species that are seen only irregularly during the night, partly because they are not especially numerous. The behavior of the more numerous squirrelfishes of the genus *Holocentrus* is less obscure. Individuals of any one

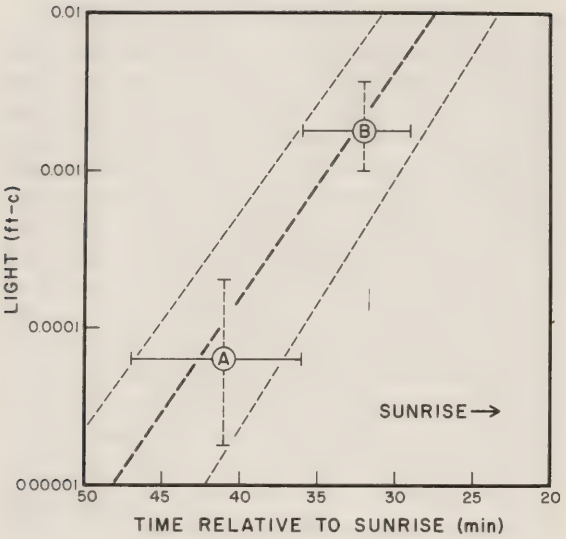

FIGURE 7.—Some characteristics of certain nocturnal fishes during morning twilight. A. *Priacanthus cruentatus*: when a certain school returned to the reef on six mornings. B. *Myripristis* spp. when the last individual descended to the reef on eight mornings. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events.

species of *Holocentrus* do not go under cover at about the same time, as is true for *Myripristis* spp. Instead, their numbers gradually diminish over a period of about 20 min during early twilight, approximately 50 to 30 min before sunrise. By the time holocentrids of the genus *Myripristis* have gone under cover, about 30 min before sunrise, the only nocturnal fishes consistently in view are scattered individuals of *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*. At this point the morning interim period has begun.

THE MORNING INTERIM PERIOD

As the midwaters are being vacated by the species of *Myripristis*, it is getting light enough for the human observer to visually distinguish details of the reef around him. It is about 30 min before sunrise, and relatively few fishes are seen. Scattered individuals of several nocturnal species, especially *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*, still hover in view close among the coral but are not active. Among diurnal fishes, a number of chaetodontids, many paired, move about close among the coral; the nocturnal colorations of many are just now giving way to their diurnal hues. Despite these active fishes, the overall aspect on the reef is quiet. Thus, the morning interim, like the evening interim, is termed the "quiet period."

About 5 min into the interim, or quiet, period, when sunrise is still about 25 min away, and when the last *Holocentrus sammara* is now under shelter, the first strong indications of increasing activity in diurnal fishes is seen. At this time the large and medium-sized surgeonfishes begin to assemble in depressions between the towering heads of the coral *Porites*. The timing of this event was recorded on six different mornings (Figure 8). These assemblages, which include

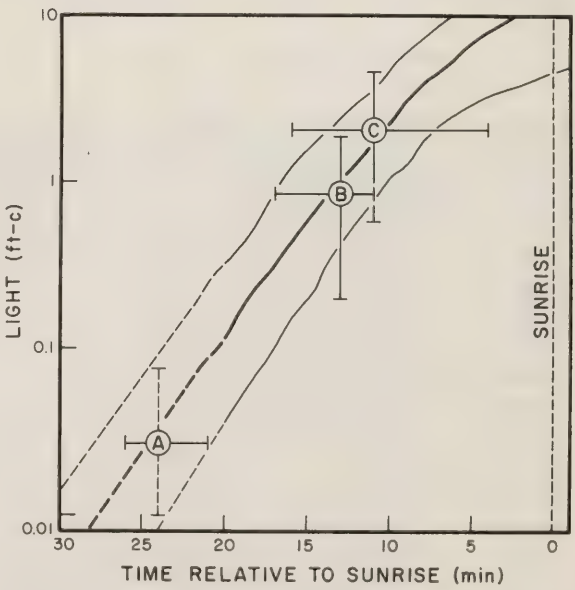

FIGURE 8.—Some characteristics of certain diurnal fishes during morning twilight. A. When species of acanthurids began to assemble in reef depressions on six mornings. B. When diurnal fishes first surged into the water column on nine mornings. C. When the first scarid appeared away from cover on nine mornings. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events.

Acanthurus achilles and *A. leucopareius,* continue to develop for about 5 min. *Zanclus canescens* soon joins in, swimming in groups of four to six, as do various chaetodontids, most notably the many species of *Chaetodon.* These become increasingly active, while at the same time staying close to the substrate. Pomacentrids, including *Pomacentrus jenkinsi* and *Plectroglyphidodon johnstonianus,* have become noticeably active close to the coral and rocks. The chaetodontid *Centropyge potteri* becomes active in the same area, and joins the pomacentrids in feeding on benthic organisms at this time. In this benthic activity, these fishes swim among the stragglers of *Apogon snyderi* and *A. menesemus,* which are now gradually going under cover.

At about 20 min before sunrise the assemblages that have been developing in depressions among the towering corals begin to rise out of the depressions and range over the reef. At first they stay close to the substrate, but then, in an action comparable in abruptness to their vacating the water column in the evening, these diurnal fishes rise 1 to 2 m above the reef. This event marks the end of the morning interim period.

THE MASS EMERGENCE OF DIURNAL FISHES

Twilight Upsurge in Activity and Reoccupation of the Water Column

The sudden surge of diurnal fishes into the water column was noted on nine mornings (Figure 8). Surgeonfishes, and to a lesser extent parrotfishes, are the predominant forms here, just as they are during the increased activity during evening twilight. As in the evening, they swim in aggregations that move back and forth 1 to 3 m over the reef, or in schools that move with seeming purpose from one location on the reef to another.

The milling assemblages.—The assemblages that develop above the reef in the morning are more segregated by species than are those that occur in these same locations during the evening. The initial surge of activity into the water column 10 to 15 min before sunrise involves mostly medium to larger herbivorous species, including surgeonfishes *Acanthurus achilles, A. leucopareius,* and *Naso lituratus.* These do not show any purposeful direction; rather, they mill about over a defined part of the reef. Also swimming in and around these assemblages are a number of larger diurnal fishes that occur as individuals, or groups of two or three fish: these include the filefish *Cantherines dumerili,* the triggerfishes *Sufflamen bursa* and *Melichthys niger,* and the parrotfishes *Scarus perspicillatus* and *S. rubroviolaceus.*

The time that the first parrotfish was seen was noted on nine different mornings (Figure 8). This observation included all species, yet *S. perspicillatus* or *S. rubroviolaceus,* the two largest species, were seen first in five of the nine instances, despite their being by far the least numerous species of the genus *Scarus.* The smaller, but much more numerous *Scarus* species, *S. sordidus, S. dubius,* and *S. taeniurus,* generally appeared later. During the time that the smaller parrotfishes are appearing, the remnants of numerous mucous envelopes, in which many of them had spent the night (see, for example, Winn, 1955; Casimir, 1971), drift about close to the substrate.

The twilight migrations.—Just as they do during evening twilight, many species migrate from one location on the reef to another at this time. As in the evening, they travel in schools that frequently are drawn out as long processions. Again, specific routes are followed morning after morning, indicating that well-defined patterns exist. Although these patterns remain obscure for most participants, some individuals clearly reverse their evening direction. Thus, having spent the night sheltered on the shallower parts of the reef, many individuals of the plankton-feeding surgeonfish *Naso hexacanthus,* along with many of the damselfish *Chromis verater,* return to their deeper water feeding grounds high above the offshore edge of the reef. As mentioned above, this pattern is obscured by the many other individuals of these species that do not migrate inshore at nightfall, but instead spend the night sheltered on the deeper parts of

the reef, directly below their midwater feeding grounds.

Just as they do in the evening, many smaller herbivores, including the surgeonfishes *Zebrasoma flavescens* and *Ctenochaetus strigosus*, as well as the parrotfish *Scarus sordidus*, migrate from one area to another, but the patterns are not yet defined. Again, the picture is obscured by the many other individuals of these same species throughout the study areas that do not join these migrations. Thus, as in the evening, it remains unknown just what sort of redistribution most of these fishes achieve. Nevertheless, the patterns seem to relate to the transition toward the diurnal situation.

Ascent of the Plankton-Feeding Damselfishes

Adults of the larger plankton-feeding damselfishes, *Abudefduf abdominalis*, *Chromis ovalis*, *C. verater*, and *Dascyllus albisella*, join the surge of diurnal fishes that rise into the water column 10 to 15 min before sunrise. Because they all ascend above the reef at about the same rate, the most readily observed, *D. albisella*, is representative. On five mornings, stationed in one location where the water was 8 m deep, I noted when a particular aggregation of *D. albisella* was clear of cover, and then as it gradually ascended into the water column, I estimated when it had attained levels of 3 m, and (on three mornings) 5 m above the reef (Figure 9).

The smaller plankton-feeding damselfishes *Chromis leucurus* and *C. vanderbilti* rise above the reef later than do these larger species. On nine mornings, at a variety of locations, I noted when the first individual of *C. leucurus* moved out away from shelter (Figure 10). These fish remained in about this position, solitary and with shelter close at hand, for some time; at 15 min after sunrise they had moved a little farther from shelter, but otherwise their position was unchanged. *C. vanderbilti* follows an even later schedule. On the one occasion that it was recorded, solitary individuals first appeared close to shelter at 1 min after sunrise, and 11 min later had just begun to aggregate in pockets among the rocks.

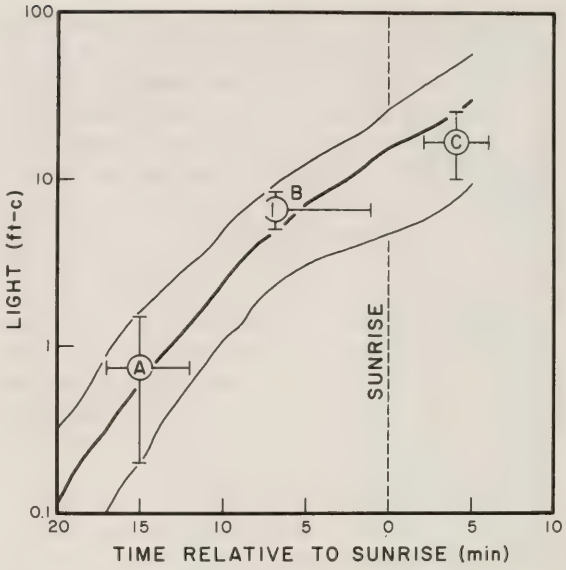

FIGURE 9.—Ascent of an aggregation of *Dascyllus albisella* into the water column during morning twilight. A. When the aggregation was first clear of cover above the reef on five mornings. B. When the aggregation had risen to 3 m above the reef on five mornings. C. When the aggregation had risen to 5 m above the reef on three mornings. For explanation of symbols, see legends for Figures 2 and 4, except that this figure represents morning events.

Emergence of Other Diurnal Fishes

Throughout the time that the diurnal fishes noted above are resuming activity on the reef, the many sedentary diurnal fishes become increasingly evident, including the hawkfishes *Paracirrhites forsteri*, *P. arcatus*, and *Cirrhitops fasciatus* and also the blennies *Exallias brevis* and *Cirripectus variolosus*. These begin moving out from shelter during the interim period, but so unobtrusively that their initial appearance usually goes unnoticed.

When the milling assemblages and migrating schools dominate the scene, additional fishes become active close among the rocks and corals, including the triggerfishes *Sufflamen bursa* and *Rhinecanthus rectangulus*, as well as the filefishes *Cantherines sandwichiensis* and *Pervagor spilosoma*. These too, being scattered and relatively inconspicuous, often go unnoticed at first appearance.

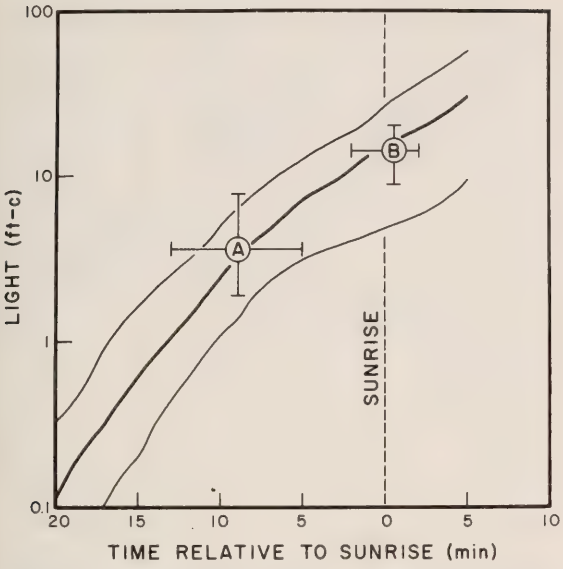

FIGURE 10.—Some characteristics of certain diurnal fishes during morning twilight. A. *Chromis leucurus*: when the first individual left cover on nine mornings. B. *Acanthurus nigrofuscus*: when individuals first appeared in school above the reef on three mornings. For explanation of symbols, see legend for Figure 2, except that this figure represents morning events.

Late Risers

Observations on Acanthurus nigrofuscus.—The assemblages of larger and medium-sized surgeonfishes that have been swimming above the reef since the initial upsurge in activity, begin to break up about the time of sunrise. Initially these aggregations become less active, then dissolve into smaller, discrete groups, now closer to the sea floor, that increasingly range out over the reef. Soon they assume activity typical of daylight. At about the time that these aggregations are breaking up, the small surgeonfish *Acanthurus nigrofuscus* makes its first appearance. Soon after, individuals of this species assemble in large schools over the reef and proceed to follow a course of action much like that taken earlier by their larger relatives. The initial appearance of *A. nigrofuscus* in a school above the reef was noted on three occasions (Figure 10). They maintain these large, active schools, as did the large species, for about 20 min, when finally these schools too dissolve into smaller discrete groups that range out over the reef.

Observations on Thalassoma duperrey.—As is true in the Gulf of California (Hobson, 1965, 1968), the smaller labrids are among the last diurnal fishes to become active in the morning. The initial appearance of the ubiquitous *Thalassoma duperrey* in the morning is representative of this group, just as is its cover-seeking in the evening. It is much easier to recognize the first individual to appear in the morning than the last individual to take cover in the evening, and on 16 mornings I noted the first *T. duperrey* to become active in my immediate surroundings (Figure 11). These fish are often unmistakable when they are just resuming activity; for several seconds after emerging from their resting places many "yawn," opening the mouth wide, and "stretch," drawing their body into various contortions.

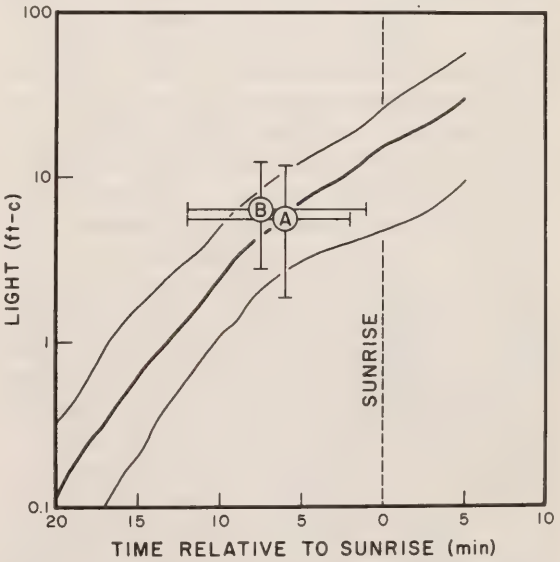

FIGURE 11.—Some characteristics of certain labrids during morning twilight. A. *Thalassoma duperrey*: when the first individual left cover on 16 mornings. B. *Labroides phthirophagus*: when the first individual left cover on nine mornings. For explanation of symbols, see legend for Figure 2, except that this figure represents morning events.

Observations on Labroides phthirophagus.—In describing evening cover-seeking by *Labroides phthirophagus* above, data are presented on just one individual. At least five individuals of this species are involved in the nine observations of the initial morning appearance (Figure 11).

Other fishes seeking cleaning from this species often hover in typical soliciting fashion at the cleaning stations (see Losey, 1971) for some time before the cleaners have made their initial morning appearance.

SUMMARY

The data presented above are summarized in Figures 12 and 13.

DISCUSSION

Most fishes on the reefs at Kona behave differently in daylight than they do at night, and during twilight their actions express a transition between these two modes of behavior. In essence, we are concerned with predominantly diurnal or nocturnal fishes changing from active to relatively inactive states, or the reverse, and the influence that certain characteristics of twilight itself have on these actions. These considerations underlie the following discussion.

FEEDING LOCATIONS VERSUS SHELTER LOCATIONS

The daily activities of tropical reef fishes show the overriding influence of two primary concerns: to eat and to avoid being eaten. Reef fishes must contend with predators at all times, but during those periods of day when they are active their actions seem dominated by their own feeding. On the other hand, during those periods of the day when they are relatively inactive, resting, their major consideration seems to be security. Thus, for example, the small parrotfish *Scarus taeniurus* grazes in exposed positions during daylight, but rests in coral crevices at night, often encased in a mucous envelope. Winn and Bardach (1959) discussed the function of the mucous envelope as a defense against nocturnal predators.

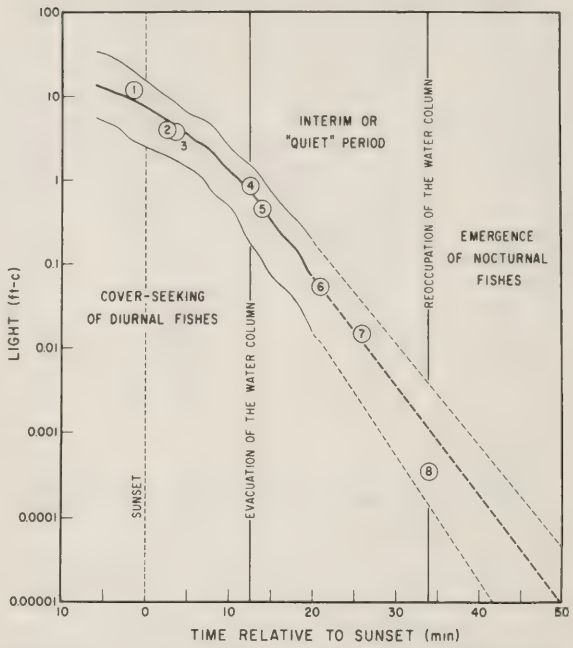

FIGURE 12.—Summary of events during the evening transition period. For explanation of symbols, see legends for Figures 2, 4, and 5. In addition, numbered points represent mean values for events. 1) When the last *Thalassoma duperrey* took cover on five evenings. 2) When a certain *Labroides phthirophagus* took cover on five evenings. 3) When the last *Chromis leucurus* took cover on three evenings. 4) Abrupt vacating of water column by diurnal fishes; the beginning of the interim, or "quiet," period: 12 evenings. 5) When *Apogon snyderi* first left cover on four evenings. 6) When *Apogon menesemus* first left cover on five evenings. 7) When *Holocentrus sammara* first left cover on four evenings. 8) When *Myripristis* spp. abruptly appeared in large numbers above the reef; the end of the interim, or "quiet," period: eight evenings.

Tropical reef fishes exhibit either one of two general means of reducing predation during their inactive periods: they school or they seek cover (Hobson, 1968). Thus, many fishes that forage at night, including various clupeids, pomadasyds, mullids, lutjanids, and carangids, characteristically spend the day in large inactive schools that hover in exposed positions on or near the reef. The advantage of such schools in reducing predation was discussed earlier (Hobson, 1968). Significantly, no diurnal fish is known

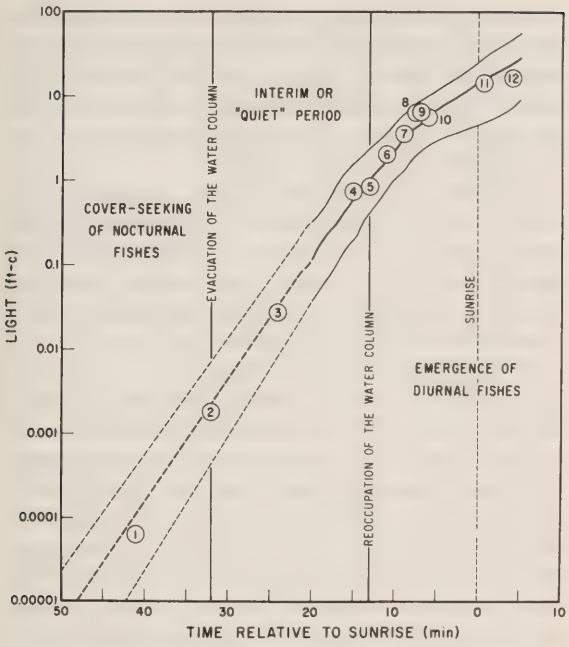

FIGURE 13.—Summary of events during the morning transition period. For explanation of symbols, see legends for Figures 2, 4, and 5, except that this figure represents morning events; in addition numbered points represent mean values for events. 1) When a particular school of *Priacanthus cruentatus* returned to the reef on six mornings. 2) When last *Myripristis* spp. took cover on reef; the beginning of the interim, or "quiet," period: eight mornings. 3) When acanthurids began assembling in depressions in the reef on six mornings. 4) When an aggregation of *Dascyllus albisella* in a particular location had moved away from cover, above the reef, on five mornings. 5) When diurnal fishes first surged 1 to 2 m into the water column; end of the interim, or "quiet," period: nine mornings. 6) When the first scarid appeared away from cover on nine mornings. 7) When the aggregation of *Dascyllus albisella* (see #4), had risen 3 m above the reef on five mornings. 8) When *Chromis leucurus* first left cover on nine mornings. 9) When *Labroides phthirophagus* first left cover on nine mornings. 10) When *Thalassoma duperrey* first left cover on 16 mornings. 11) When *Acanthurus nigrofuscus* first appeared in school above the reef on three mornings. 12) When the aggregation of *Dascyllus albisella* (see #4 and #7) was 5 m above the reef on three mornings.

to similarly school during its nocturnal inactive period. Fishes that form large schools in exposed locations when inactive are not well represented on Kona reefs; possible reasons are given below. The other means of attaining security while inactive—seeking shelter under rocks or coral—is characteristic of many diurnal as well as nocturnal fishes, including labrids, scarids, balistids, holocentrids, and apogonids. This second tactic is employed by most reef fishes in Kona. The advantage of cover in reducing predation is obvious. Some of the nocturnal fishes, for example, species of *Myripristis* and *Holocentrus*, as well as *Priacanthus cruentatus*, characteristically aggregate under cover on the reef in daylight; in contrast, none of the diurnal species were noted to aggregate when sheltered in their nocturnal resting spots.

Each of the wide variety of fishes on the Kona reef has its own specific feeding habits (Hobson, in preparation), and these relate in large part to where each is active. A suitable feeding location for any given species may or may not be near areas that offer it suitable security during its inactive period. Consequently, the major actions of these fishes characteristic of twilight relate to moving between feeding locations and shelter locations.

TWILIGHT REDISTRIBUTION

Most of the readily observed movements of Kona reef fishes during twilight fit within a framework of three broad, overlapping categories: 1) individuals of some species migrate extensively between offshore feeding grounds and shelter locations on the reef; 2) other species migrate from one part of the reef to another; and 3) still others make short but well-defined vertical migrations between plankton-feeding locations in the water column and shelter locations on the reef below. These movements are all performed by fishes swimming in groups. The movements of most reef fishes, which remain poorly known, do not seem referable to any of these categories; nevertheless, limited evidence indicates that at least many of them follow well-defined patterns of some sort. There is much overlap between the different categories and the activity of many species comprise elements of more than one type. It is for convenience in

presentation that each category is discussed separately below.

Offshore Migrations

Nocturnal fishes.—In many seas, certain reef fishes are known to make extensive feeding migrations away from the reef at nightfall; outstanding examples include certain clupeids, pomadasyids, carangids, and other schooling fishes in the Gulf of California (Hobson, 1965, 1968) and tropical Atlantic (Starck and Davis, 1966). These migrations are best known among those nocturnal predators that school on or near the reef during their inactive periods. Although such schooling fishes and their offshore migrations during twilight are a major characteristic of some areas, they are not prominent on Kona reefs. This is understandable. The reefs where these schooling fishes and their offshore migrations are so pronounced in the Gulf of California and in the tropical Atlantic are surrounded by extensive open sand flats or grass beds. These vast stretches are nocturnal feeding grounds of the fishes that migrate away from the reefs. The importance of proximate feeding grounds of this sort to such fishes is well known (Longley and Hildebrand, 1941; Randall, 1963; Hobson, 1968). Similar feeding grounds do not surround Kona reefs, which are instead bordered by a precipitious drop into deep water. Not surprisingly, the relatively few species that migrate offshore at nightfall from Kona reefs, including *Priacanthus cruentatus* and *Myripristis* spp., seek open-water prey. Furthermore, whereas fishes migrating over the extensive sand flats and grass beds adjacent to reefs elsewhere often travel considerable distances (Starck and Davis, 1966; Hobson, 1968), comparable data are not available for *Priacanthus* and *Myripristis*. It is possible that these fishes do not go much beyond the outer edge of the reef, an area known to be a rich feeding ground for diurnal plankton-feeding fishes (see below).

Diurnal fishes.—Offshore feeding migrations comparable to those made by nocturnal fishes have not been reported for diurnal fishes. In the Gulf of California, the exodus of fishes away from the reef during twilight, transforming the stretches of open sand offshore into centers of activity, is strictly a nocturnal phenomenon; there is no diurnal equivalent, as these open expanses are comparatively without active fishes in daylight (Hobson, 1968).

In Kona, several diurnal fishes, including some individuals of the surgeonfish *Naso hexacanthus* and the damselfish *Chromis verater*, migrate to the offshore edge of the reef during morning twilight. They swim to where the seaward reef-face drops abruptly to great depths and here become part of a large assemblage of plankton-feeding fishes. Apparently plankton is exceptionally rich in this area. The migrations seem to terminate here, but the larger *Naso hexacanthus*, and perhaps other species, periodically range farther offshore during the day. During evening twilight many individuals of these species return inshore to the shallower parts of the reef, a pattern obscured by the many other individuals of these species that shelter themselves on the offshore parts of the reef, below their midwater feeding grounds. It may be that there is not enough suitable cover here to accommodate all of the many fishes that concentrate to feed in this location. This would account for the fact that while some shelter themselves here, others migrate from other areas.

Intrareef Migrations

Conspicuous elements of the transition period are the long drawn-out processions that migrate from one point on the reef to another, following the same routes day after day. Although the redistribution pattern achieved by these movements remains undefined, the phenomenon seems limited to herbivorous fishes, especially the small to medium-sized acanthurids and scarids, and to some plankton feeders. Herbivorous reef fishes are widely reported to be strictly diurnal (Hobson, 1965, 1968; Starck and Davis, 1966). The migratory patterns shown by these fishes are obscured by the many other individuals of the migrating species that do not join these movements.

Some herbivorous species, for example certain parrotfishes (see Bardach, 1958), range far

across the reef in schools while grazing on benthic algae during the day. The intrareef migrations during evening twilight of such fishes may be a return from such excursions to established resting areas at day's end.

Vertical Migrations

The movements discussed so far involve fishes that traverse considerable distances. Many other fishes, some diurnal, others nocturnal, move between feeding grounds and shelter locations in a well-defined pattern that covers no more than a few meters. These are the many plankton feeders that forage in the water column, and find shelter on the reef directly below. Some species, like the diurnal *Naso hexacanthus* and the nocturnal *Myripristis argyromus*, both discussed above, undertake such vertical movements but also make extensive lateral excursions across the reef and beyond. Nevertheless, many plankton feeders, especially smaller species like *Dascyllus albisella*, restrict their activity to a limited area on the reef. Restricted though these movements may be, they follow patterns as well defined as any of those discussed above.

These plankton feeders are either diurnal or nocturnal. Without overlap, those feeding in daylight are inactive after dark, and those feeding at night are inactive in daylight. The respective feeding periods of the two groups are separated by the 15 to 20 min interim, or quiet, period. I noted a similar absence of overlap between diurnal and nocturnal plankton feeders in the Gulf of California (Hobson, 1968), as did Starck and Davis (1966) in the tropical Atlantic. Obviously conditions of plankton feeding differ between day and night. Emery (1968) reported that the composition of plankton over Florida reefs differs between day and night, and I found the same true in Kona (Hobson, in preparation).

Twilight Movements of Other Reef Fishes

The patterns of movement described above are readily recognized because each involves many individual fish moving together. Most reef fishes do not operate in large assemblages but instead are active solitarily or in small groups. Unifying patterns in such species are difficult to recognize, because many discrete units are simultaneously behaving independently at different points on the reef. Nevertheless, limited data show that patterns do exist. Probably the movements of some fall into the broad categories outlined above, but the actions of others, once recognized, probably would represent additional categories. Chaetodontids, labrids, pomacentrids, scarids, balistids, and other diurnal species, as well as many holocentrids, apogonids, scorpaenids, and other nocturnal fishes, all display distinctive nocturnal and diurnal habits. The twilight activities of most of these fishes do not include extensive movements; most change from an active to a relatively inactive state, or the reverse, within a limited area on the reef. Data presented in this report show well-defined temporal patterns in their seeking and everging from cover. Limited additional data indicate that in at least many of these fishes the patterns also have a strong spatial element: consider, for example, the circumstance that at least some individuals of *Thalassoma duperrey* and other species occupy specific resting spots at nightfall.

PATTERNS OF TWILIGHT ACTIVITY

I have developed the thesis that activity of most Kona reef fishes during twilight relates to a transition between diurnal and nocturnal modes of behavior. If these fishes were concerned only with shifting from one mode of behavior to another, the timing of the various transition events could well as not be random. In fact, however, the transition events proceed in an established, well-defined sequence, with characteristics indicating that some force exerts a strong controlling influence. The general pattern has been outlined above (Figures 12 and 13). Some additional characteristics of the transition events warrant discussion.

Fish Size as Expressed in Transition Activity

The time during the transition at which a given fish joins certain of the activities is related to that fish's size. During evening twilight

some of the transition activities are performed by the smaller fishes first. Thus, for example, the increased tendency of many fishes to aggregate, as seen especially in acanthurids and scarids, occurs first in the smallest species of the respective groups: *Acanthurus nigrofuscus* among the acanthurids, and *Scarus taeniurus* among the scarids. Consider too the plankton-feeding damselfishes, which during the transition period progressively descend closer to the sea floor and finally take cover on the reef. The smallest species, *Chromis vanderbilti*, is first to seek cover, and the next smallest, *C. leucurus*, is second. The other, larger damselfish species follow later. Similarly, the smallest of the surgeonfishes, *Acanthurus nigrofuscus*, is the first of that family to go under cover, and the others follow in order roughly corresponding to increasing size. Most acanthurids on the reef are of about the same size and therefore show similar timing in seeking cover; nevertheless, the larger species, like *A. dussumieri*, are the last to settle down. The same pattern occurs among the filefishes, where the smaller *Cantherines sandwichiensis* takes cover long before the larger *C. dumerili;* and among the parrotfishes, where the smallest, *Scarus taeniurus*, is no longer seen when such larger relatives as *S. rubroviolaceus* and *S. perspicillatus* are still active. The effect operates within species, just as it does between species; thus, for example, large adults of *Scarus rubroviolaceus* are still active long after all the small juveniles of this species have gone under cover.

In the morning the situation in these same species is reversed. The larger individuals are the first of the diurnal fishes to emerge from cover, and the others appear in order roughly according to decreasing size to perform their characteristic transition activity.

It remains uncertain to what extent fish size relates to the transition activity of nocturnal fishes. *Holocentrus sammara*, *Apogon menesemus*, and *A. snyderi*, which are consistently the first nocturnal species to leave shelter in the evening and the last to seek shelter in the morning, are the largest of their respective groups common in Kona; however, additional data are lacking.

Increased Activity During Twilight

One senses a marked increase in activity among fishes at two times during the twilight periods: in the evening, from just before sunset to about the time that the diurnal fishes abandon the water column, and in the morning, from the time the diurnal fishes reoccupy the water column to just after sunrise. This impression of heightened activity derives mostly from a combination of the following: 1) fishes migrating from one location to another; 2) increased territorial aggression (evening only); and 3) an increased tendency to aggregate in locations more visible to the observer.

Migrations.—The migrations are discussed above. Their contribution to a general impression of increased activity is obvious.

Territorial aggression.—A minor element of the increased activity during evening twilight is increased territorial aggression. During the day there are frequent territorial disputes among many of these fishes, often, if not generally, relating to feeding areas; this is a frequent source of conflict among the acanthurids (see, for example, Jones, 1968). Aggression during evening twilight, which was noted only in diurnal fishes, seems unrelated to feeding; rather, it may express conflict over resting spots. It is significant not so much that such aggression occurs, but that there is so little of it. With such a vast number of fishes settling into resting positions on the reef at nightfall, one might expect individuals with similar requirements to compete strongly for optimum spots. That relatively little aggression of this sort occurs suggests that some mechanism establishes spatial distribution without overt conflict. One possibility is that each individual has a well-established resting spot; this is suggested by the two individual *Thalassoma duperrey* that were observed to be strongly attached to particular locations. However, this hypothesis is not widely supported. Overall, I recognized only a relatively few cases where what seemed to be the same individual returned to a particuar spot on

a number of different nights, and even these did not seem to have a long-standing attachment to such locations. More important, I was unable to recognize attachments to particular locations in most of the diurnal species that occupy resting spots when inactive. There are scattered reports of reef fishes returning to established resting spots: Winn and Bardach (1960), for example, noted that a certain species of parrotfish in Bermuda has "home caves," and Starck and Davis (1966) suspected the same to be true of two parrotfish species in Florida. Nevertheless, pending accumulation of additional data from a variety of fish groups the question on a broad scale remains unresolved.

Nocturnal fishes seeking cover in the morning were not seen in conflict over resting spots. A major general behavioral difference between diurnal and nocturnal fishes may account for this. Unlike diurnal fishes, which generally are solitary in their resting places, many nocturnal species, including *Myripristis* spp., *Holocentrus* spp., and *Priacanthus cruentatus*, aggregate in their daytime shelters.

Increased tendency to aggregate in locations more visible to the observer.—The general impression of increased activity during the periods of twilight defined above stems mainly from the many diurnal fishes that congregate one to several meters above certain parts of the reef at these times. These fishes, which concentrate over areas where at least most of them seek shelter, mill about actively, but without recognized direction. Although surgeonfishes predominate in these aggregations, species from many families of diurnal fishes are represented. However, it can be questioned whether or not this phenomenon does in fact involve increased activity. At least to some extent the fishes only appear to be more active. At this time, compared to other times of day, they are more concentrated and swim in locations that are more visible to the observer. Mostly these are gregarious species, but the groups in which they swim during midday are less visible than the twilight assemblages, being smaller, more loosely organized, and occurring closer to the substrate at many different places on the reef.

THE INFLUENCE OF PREDATORS ON TWILIGHT ACTIVITY

I have emphasized that the twilight activity in reef fishes proceeds in an established, well-defined sequence. Now I suggest that this well-ordered series of events is shaped by the threat of crepuscular predators.

In the Gulf of California (Hobson, 1965, 1968) and certain parts of the tropical Atlantic (Starck and Davis, 1966), large piscivorous fishes are primarily crepuscular. The increased vulnerability of smaller free-swimming fishes during twilight, especially those in schools, has been discussed (Hobson, 1968). Mechanisms that reduce the threat from predators during daylight and darkness apparently are less effective during the transition between these two major segments of the diel cycle. Thus attacks by large piscivores on schooling clupeids, pomadasyids, and small carangids in the Gulf of California become increasingly frequent at about the time of sunset, and peak about 20 min later. After peaking, the predation ceases, and the piscivores withdraw. Most of the schooling prey, which are nocturnal predators, then migrate to their offshore feeding grounds (Hobson, 1968). Because this activity is a dominant feature of the reef situation in the Gulf of California, one can relate it to the concurrent actions there of such smaller nonschooling fishes as labrids, pomacentrids, chaetodontids, acanthurids, and balistids. The pattern of cover-seeking in these fishes, and the subsequent emergence of such nocturnal forms as holocentrids and apogonids, follows much the same pattern in the Gulf as that of their close relatives in Kona, described in this report. Observations on the transition events in the Gulf of California were not detailed to the extent of those in Kona; nevertheless, many of the same phenomena were reported from the Gulf. For example, referring to evening observations I pointed out that labrids are among the first of the diurnal fishes there to seek cover and that the emerging *Apogon* mix with some of the diurnal fishes close among the rocks as the latter are taking cover (Hobson, 1965, 1968). I am confident that the techniques used in Kona, if

repeated in the Gulf of California, would generate data much like those presented in this report. Although the faunas of the two areas have only a few species in common, there are many generic parallels. Genera common to both areas include: *Bodianus, Thalassoma, Halichoeres,* and *Hemipteronotus* (labrids); *Abudefduf, Chromis,* and *Pomacentrus* (pomacentrids); *Chaetodon* and *Holacanthus* (chaetodontids); *Acanthurus* (acanthurids); *Balistes* and *Suffla-men* (balistids); *Holocentrus* and *Myripristis* (holocentrids); *Apogon* (apogonids); and many others. Congeners from these two widely separated areas behave similarly.

In the Gulf, one can readily relate the distances small fishes are from shelter at different times during the transition period with the concurrent attacks by large piscivores on the schooling fishes; when this piscivorous activity peaks, most of the small nonschooling fishes are under cover. As I pointed out (Hobson, 1968, p. 84), ". . . during those periods of morning and evening twilight, when schooling fishes are most heavily exploited, neither diurnal nor nocturnal plankton feeders (mostly *Chromis, Abudefduf, Myripristis* and *Apogon*) are in midwater."

Significantly, the reef fishes in Kona all are close to shelter at the time, relative to sunrise or sunset, that schooling fishes in the Gulf of California are under heaviest attack (Figures [3]14 and [4]15). At the same time that predation upsurges in the Gulf, the water column is vacated in Kona, both by nocturnal fishes during early morning twilight and by diurnal fishes during early evening twilight. Furthermore, the water column is not then reoccupied in Kona, either

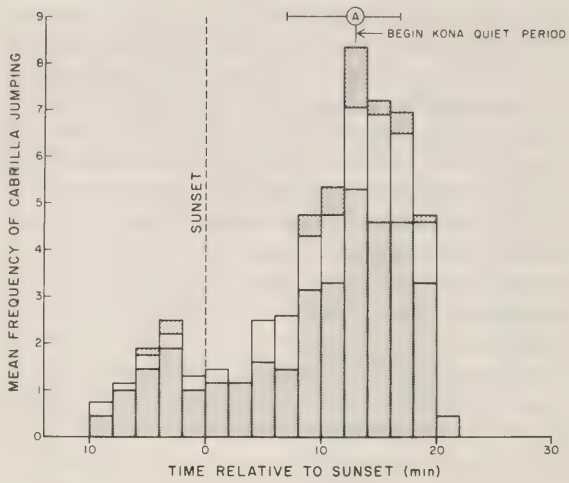

FIGURE 14.—Time of peak predation (*Mycteroperca rosacea* when preying on schooling *Harengula thrissina*) in the Gulf of California relative to the evening interim, or "quiet," period in Kona. Duration of twilight is similar in the two areas as the difference in latitude is only about 4°. Stippled area of the bars represents the frequency of attacks involving one *M. rosacea*; white area of bars, the frequency of attacks involving two to seven *M. rosacea;* hatched areas of bars, the frequency of attacks involving eight or more *M. rosacea* charging simultaneously. Also plotted is the mean (A) and the range of times, relative to sunset, that diurnal fishes vacated the water column in Kona. (For further information regarding this figure, see text footnote 3.)

[3] When preying on schooling flatiron herring, *Harengula thrissina,* in shallow water in the Gulf of California, the cabrilla, *Mycteroperca rosacea* attacks from below. Its charge carries the cabrilla up through the herring school and momentarily out of the water (see Hobson, 1968). Because the herring schools are close to the beach throughout the day and into twilight, an observer on the beach can obtain an index of predatory activity by noting the incidence of attacks—seen as cabrilla jumping out of the water amid the herring. These data were collected on seven consecutive evenings and were presented earlier (Hobson, 1968, Figure 18).

In Figure 14, I have pooled these data, and present the mean values in time relative to sunset (when presented in Hobson (1968) these data were broken down by days, and shown against time of day). The graph also reflects the fact that discrete attacks involve varying numbers of cabrilla charging simultaneously. Unfortunately, the attacks by cabrilla on herring do not provide an index of predation beyond about 20 min after sunset; at this time, with the cabrilla and other predators still highly active, the herring migrated offshore. Thus the sudden drop in attacks shown in the figure reflects the herring's departure, not a decline in predation. The predators continued to attack other schooling fishes in the area, mostly pomadasyids, for a short while longer, and these prey schools did not leave the inshore waters until the predators had withdrawn (Hobson, 1968). In any event, because the attacks by cabrilla on herring provided an index only for the initial upsurge in predatory activity, it is meaningless to relate these data to the latter stages of the Kona quiet period.

[4] Data on predation by cabrilla on flatiron herring were collected on three consecutive mornings (see Hobson, 1968). Unlike the evening situation in the Gulf of California, where the herring leave the inshore waters while the cabrilla and other predators are still highly active, in the morning the herring arrive inshore before the predators have begun feeding. Therefore, the attacks by cabrilla on flatiron herring in the morning provide an index of predatory activity spanning all of the twilight period, and thus can be related to the entire interim, or "quiet," period in Kona.

by diurnal fishes during morning twilight, or by nocturnal fishes during evening twilight, until after the time that predation in the Gulf has subsided. Thus, the time of maximum predation in the Gulf is equivalent to what is aptly called the "quiet" period in Kona. Obviously the term "quiet" would be a misnomer if applied to this part of the transition period in certain parts of the Gulf, it being the time when the schooling fishes are under heaviest attack. These schooling species, for example the herring *Harengula*, cannot take shelter under rocks or coral on the reef, as have the other smaller fishes, and thus are exposed to predators during a time when they seem to be especially vulnerable. The disadvantage of schooling fishes at this time, as compared to other potential prey of the piscivores, was pointed out earlier (Hobson, 1968). Thus, if there is an advantage in being close to shelter when predators are most effective, the actions of Kona reef fishes during twilight are adaptive to any increased threat from predators that might exist at that time.

Other behavioral characteristics of Kona reef fishes during the day-night transition period can be interpreted as mechanisms to reduce predation. If one accepts the premise that smaller fishes are more vulnerable to predation than larger ones, it is significant that smaller individuals seek cover earlier in the evening, when danger from predators apparently is progressively intensifying. The same significance can be attributed to their leaving cover later in the morning when danger from predators apparently is progressively diminishing. Consider too the increased tendency to aggregate among so many fishes that just mill over a given section of the reef. Although this behavior probably has other functions as well, it may also contribute some measure of security from predators. It was pointed out earlier (Hobson, 1968) that fishes in such aggregations attain the same protection from predators as do those in schools (if one wishes to distinguish between such assemblages).

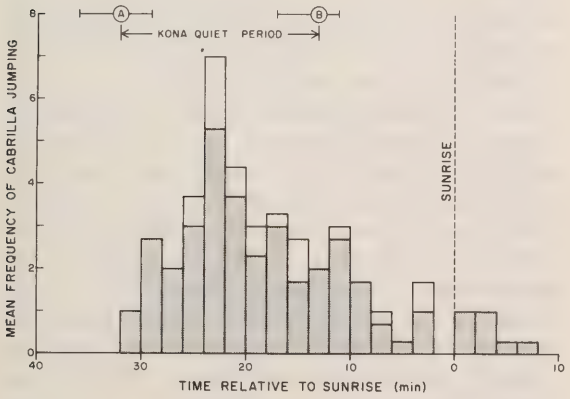

FIGURE 15.—Time of peak predation (*Mycteroperca rosacea* when preying on schooling *Harengula thrissina*) in the Gulf of California relative to the morning interim, or "quiet," period in Kona. For explanation of symbols, see legend for Figure 14. The mean and ranges of both the beginning (A) and end (B) of the Kona quiet period, defined by events described at length in this report, are plotted. (For further information regarding this figure, see text footnote 4.)

Clearly the overall pattern of activity in Kona reef fishes during twilight can be interpreted as being strongly influenced by crepuscular predators. Yet, critics of this hypothesis can point out that an obvious piscivorous threat is absent, at least relatively so when the Kona habitats are compared to those of the Gulf of California.

Hawaiian reefs have been known to be lacking in some of the major predatory fish-groups that are common on most other tropical Pacific reefs. Most notable among these are the shallow water groupers (Serranidae) and snappers (Lutjanidae)—Gosline and Brock, 1960; Randall and Brock, 1960. There are several large carangid species in Hawaii, but the only one that is numerous in Kona, *Caranx melampygus*, is represented mostly by small individuals. Possibly heavy pressure from fishermen along Hawaiian shores keeps the numbers of large carangids at a low level. Because the major piscivorous fishes on the reef at Kona (aside from some of the moray eels, which probably do not prey significantly on free-swimming fishes) are relatively small, they do not seriously threaten the adults of the species being considered here. These include such predators as *Fistularia petimba*, *Aulostomus chinensis*, *Paracirrhites forsteri*, *Parupeneus chryserydros*, and *Bothus mancus*. The predatory activity of these and other species

is detailed elsewhere (Hobson, in preparation). The occasional occurrence during twilight of large barracuda, *Sphyraena barracuda*, and sharks, especially *Carcharhinus milberti*, would not seem to have much impact on the general behavior patterns of the reef fishes. However, any behavior that reduces vulnerability to predators certainly would enhance survival on the occasions when such predators do appear, and the effect of this circumstance may be greater than is readily apparent. Nevertheless, with neither schooling prey nor the predators that exploit them being major elements of the fauna, the vigorous interactions such fishes so prominently generate during twilight in the Gulf of California are essentially missing in Kona.

The absence of large piscivores on the Kona reef as compared, for example, with the Gulf of California, may bear on the relative scarcity in Kona of prey fishes in large schools. Reason for the relative absence of such fishes in Kona was discussed above. The many schooling prey in the Gulf of California was held to be a major factor in the occurrence there of so many large piscivores (Hobson, 1968). For whatever reason these faunal elements are missing in Kona, the question remains: if the threat from predators strongly influences the well-defined sequence in which fishes in the Gulf seek and leave cover during the day-night transition, how is it that reef fishes in Kona show essentially the same pattern when the threat of large piscivores to them is comparatively mild?

We have been focusing on the situations in Kona and the Gulf of California, when in fact it seems that related fishes on most, if not all, tropical reefs, show similar behavior during twilight. Data are lacking for most areas, so this conclusion remains tentative. Nevertheless, not only do related fishes common to Kona and the Gulf of California behave similarly, as described above, but limited data from other seas, including the tropical Atlantic (Starck and Davis, 1966) show essentially the same pattern. The similar pattern of events in these widely separated areas indicates a long evolution that in any one locality transcends the existing situation, even the existing species.

One would expect predator-prey relations among fishes to have responded similarly throughout time to certain basic, unchanging phenomena. Among others, these phenomena would have included the characteristics of light underwater and the effect of these characteristics on visually feeding predators at different times of the day, as well as the probable difficulties such predators experience in choosing a target from among the many confronting them in a fish school (Allen, 1920a, 1920b; Hobson, 1968; and others). With this common heritage, it would be surprising if behavior patterns relating to predator-prey interactions did not show today deep-rooted parallels on even widely separated reefs. I suggest, therefore, that the behavior of tropical reef fishes during twilight in all seas, including Kona, reflects the impact of a historic threat from predators.

CONCLUSIONS

1. At least most of the reef fishes at Kona, Hawaii, behave differently in daylight than they do at night, and during twilight their actions express a transition between these two modes of behavior. Most of these fishes are either diurnal or nocturnal, with the diurnal species relatively inactive at night and the nocturnal species relatively inactive in daylight.

2. During their period of major activity, the actions of these fishes are dominated by behavior relating to their own feeding, and often this takes them to specific feeding grounds. During their inactive periods their behavior relates strongly to their own security, and usually they take shelter. Consequently, the actions of these fishes during twilight relate primarily to moving between feeding locations and shelter locations.

3. The twilight movements of many of these fishes involve well-defined migrations. A) Some members of certain nocturnal species migrate extensively between shelter locations on the reef and feeding grounds offshore; species in this category include *Myripristis* spp. and *Priacanthus cruentatus*. B) Some members of certain other species migrate between shelter locations on one part of the reef and feeding grounds on another; species in this category are mostly di-

urnal herbivores and plankton feeders, including certain acanthurids, scarids, and pomacentrids. C) Many small plankton-feeding species make short, but well-defined vertical migrations between shelter locations on the reef and feeding locations in the water column directly above; diurnal species in this category include certain pomacentrids and chaetodontids, and nocturnal species include certain apogonids and holocentrids.

4. Activity associated with the transitions from day to night, and from night to day, proceeds in an established, well-defined sequence. Both evening and morning periods of changeover comprise three distinct segments. In the evening, these are: 1) *the shelter-seeking of the diurnal fishes* (from about 30 min before sunset to about 13 min after sunset), which ends when the last group of diurnal fishes still milling above the reef, mostly acanthurids, abruptly descend to cover; 2) *the evening interim, or "quiet," period* (beginning about 13 min after sunset and ending about 20 min later), which is characterized by the water column being essentially deserted of fishes; and 3) *the emergence of the nocturnal fishes* (from about 33 to 50 min after sunset), which begins when the surge of nocturnal fishes, mostly *Myripristis* spp., rise into the water column. In the morning, the sequence is reversed, being: 1) *the shelter-seeking of the nocturnal fishes* (from about 50 to 30 min before sunrise), which ends when the last of the nocturnal fishes in the water column, usually *Myripristis* spp., have descended to cover; 2) *the morning interim, or "quiet," period* (beginning about 33 min before sunrise and ending about 20 min later), when the water column is essentially deserted; and 3) *the emergence of the diurnal fishes* (from about 13 min before sunrise to a point soon after sunrise), which begins when the surge of diurnal fishes, mostly acanthurids, rise into the water column.

5. In the evening, diurnal fishes, both within and between species, seek cover in an order that corresponds roughly to increasing size. That is, the larger fishes seek cover last. In the morning, the same fishes emerge from cover in an order that corresponds roughly to decreasing size. That is, the larger fishes emerge from cover first.

6. There is some territorial aggression among diurnal fishes during evening twilight that expresses conflict over resting spots. However, the aggression is minimal considering how many fishes settle into resting positions on the reef at this time. Limited evidence suggests that overt conflict is reduced because at least some individuals have established resting spots.

7. Reef fishes are most vulnerable to predators during twilight because mechanisms that reduce predation during the day and night are less effective during the transition between these two major segments of the diel cycle. The interim, or "quiet," period in Kona is the time of greatest potential danger and corresponds in time relative to sunrise and sunset to the period when schooling fishes in the Gulf of California are under heaviest attack. Similar overt predator-prey interactions are relatively infrequent at this time in Kona because the schooling prey and the predators that exploit them are not major elements of the Kona fauna.

8. The well-ordered pattern of twilight activity among Kona reef fishes, which is essentially the same among tropical reef fishes in other seas, has been shaped by a historic threat from crepuscular predators. In areas where predators are only a relatively mild threat, as in Kona, twilight activity follows the same pattern as it does in areas where predators are a severe threat, as in the Gulf of California. Because predator-prey relations among fishes have responded throughout time to certain basic, unchanging phenomena, the similarity of twilight activity patterns among fishes on widely separated reefs today is the result of a long evolution that in any one area transcends the existing situation and species.

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CONSIDERATION OF THREE PROPOSED MODELS OF THE MIGRATION OF YOUNG SKIPJACK TUNA (*KATSUWONUS PELAMIS*) INTO THE EASTERN PACIFIC OCEAN[1]

F. WILLIAMS[2]

ABSTRACT

Previous evidence suggested that most exploited skipjack tuna (*Katsuwonus pelamis*) in in the eastern Pacific Ocean have a central Pacific spawning origin. Three models are now proposed of the migration of young skipjack into eastern Pacific fishery areas; these are (i) the active migration model, (ii) the passive migration model, and (iii) the gyral migration model. Data utilized and theories advanced in the detailed development of the models are discussed. Mechanisms and timing in all three migration models are dependent on oceanographic conditions and events in the central-east Pacific, which thus have a controlling effect on migration success of incoming young fish. Current skipjack research cruises, in part designed to test the validity of the models, are outlined.

Skipjack tuna (*Katsuwonus pelamis*) are widely distributed in tropical and subtropical surface waters of world oceans. In the Pacific Ocean there are three principal fisheries: the Japanese home islands fishery, including the Ryukyu-Tokara-Izu-Bonin Islands (1956-1969, range 87,000-252,000 short tons); the Hawaiian Islands fishery (1956-1969, range 3,000-8,000 short tons); and the eastern Pacific fishery from California to northern Chile (1956-1970, range 52,000-132,000 short tons). In addition, there are skipjack fisheries off Taiwan and the Philippines, developing ones of various sizes in Micronesia, Melanesia, and Indonesia, and subsistence fisheries in many other island groups, such as the Society-Tuamotu Islands. With the regulation of yellowfin catches in the eastern Pacific through an annual catch quota and the general decline in Japanese longline catch rates of tunas, the fishing industry has been showing increased interest in skipjack for a greater share of total tuna catches.

Fujino (1967, 1970, and in press) has shown that genetic studies indicate a subpopulation of skipjack in the western Pacific distinct from that present in the central-east Pacific. Seasonal mixing of the two subpopulations, or replacement one by the other, is considered to take place in the area immediately to the east of an arc through the New Hebrides-Solomon-Caroline-Mariana-Bonin Islands chains to the waters off the northeast coast of Japan.

The hypothesis on North Pacific skipjack advanced by Kawasaki (1965a, b) proposed a transpacific population with a common element and radiation outwards of juveniles from a central Pacific spawning area with eventual return to that area of sexually mature fish. This aspect of Kawasaki's hypothesis does not seem tenable, in view of Fujino's work. It is possible though that Pacific-wide changes in environmental conditions may cause apparently similar fluctuations in skipjack abundance in different areas through effects on recruitment and distribution.

Schaefer (1963) and Rothschild (1965) reported on the structure of skipjack populations in the central-east Pacific and stated that skipjack in the eastern Pacific fishery have a central Pacific origin. This inference was based primarily on the indicated general lack of spawning

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in the eastern Pacific (east of long 130°W), by few fish with fully developed gonads (Schaefer and Orange, 1956; Orange, 1961) and few larvae (Matsumoto, 1958; Klawe, 1963), and the occurrence of some long distance tag returns indicating movements from Baja California to the central Pacific, including the Hawaiian Islands (Schaefer, 1963; Inter-American Tropical Tuna Commission, 1964). (Subsequent data on skipjack larval distribution and tagging have supported the inference for a central Pacific origin.) Schaefer's and Rothschild's opinions differed, however, as to whether skipjack from south of the equator entered into this common genetic pool. Fujino (1970) indicated there was no genetic evidence to suggest South Pacific skipjack are not part of the central-east Pacific subpopulation(s) and also stated that present evidence for any differences between skipjack from varying parts of the central-east Pacific (Hawaiian Islands, Line Islands, Ecuador, Baja California) is very slight.

Rothschild (1965) generated a hypothesis on the movements of skipjack within the central-east Pacific (Figure 1). He postulated that skipjack juveniles in the central Pacific are continually dispersing from that region and that a large component of them move eastward into the eastern Pacific, where one contingent enters the Baja California fishery and the other the Central-South American fishery. Recruitment to these fisheries commences at about 35-40 cm (Rothschild, 1965; Joseph and Calkins, 1969). The fish remain in the eastern Pacific until they are maturing or mature at 40-65 cm, which probably is for 12 months or less, but only rarely longer than this. Thereafter, the fish leave the region and return to the presumed spawning grounds in the central Pacific and do not usually return to the eastern Pacific surface fishery.

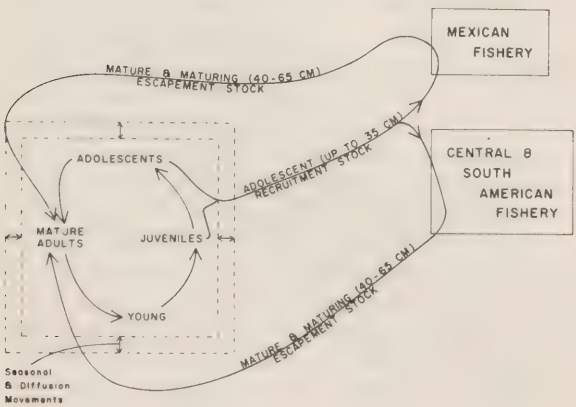


FIGURE 1.—Diagram showing the flow of skipjack between the central Pacific and the Mexican and South American fisheries of the eastern Pacific Ocean (from Rothschild, 1965, Figure 2).

The boundary between the two eastern Pacific fishery groups appears to be centered on the Gulf of Tehauntepec, with the northern fishery mainly off Baja California and the southern one mainly off Central America and Ecuador. There appears to be little mixing between these fishery groups as seen by lack of intergroup returns (Joseph and Calkins, 1969; Fink and Bayliff, 1970) and morphometric analysis (Hennemuth, 1959) even though genetic data (Barrett and Tsuyuki, 1967; Fujino, 1970) show no gross intergroup differences. The degree of geographic separation of the groups varies considerably from year to year (Williams, 1970).

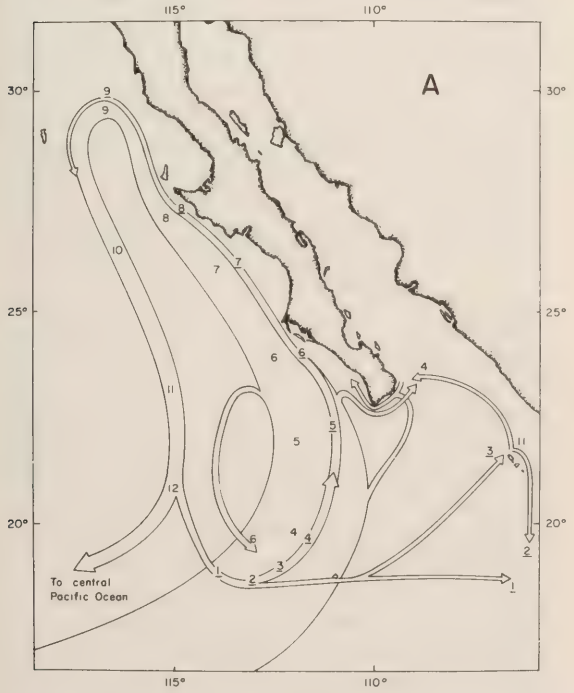
According to Rothschild (1965) the mechanism causing the split into northern and southern fishery groups could be many and not fixed in time or space. The extent to which they split the skipjack into the northern and southern groups could be a function of the north-south and temporal distribution of the incoming eastward-moving recruits. One possible splitting mechanism was considered to be the warmwater cell (surface temperatures $>28°C$) in the vicinity of lat 15°N off the Central American coast (see monthly average temperature conditions, Wyrtki, 1964). Blackburn (1962) suggested that this same warmwater cell impeded north-south movement and intermingling of the groups, the extent of which varied with surface temperature from year to year. Williams (1970) has shown that in the eastern Pacific, skipjack occur at all temperatures $>17°C$ with the majority from 20° to 30°C, though apparent abundance was only high up to 29°C. This increase of 1°C, from 28° to 29°C, in the limiting temperature for skipjack in quantity is important. The monthly average temperature charts of Wyrtki

(1964) show the area of water >29°C is much less extensive than that >28°C, particularly offshore to the westward, and also in duration, e.g., in April-May 28°C water normally extends out to long 118°-119°W, but 29°C water only to long 102°-103°W. Even if the 28°C water was accepted as a splitting mechanism, it is shown in a subsequent section that not being fully developed in offshore extent (to long 120°W) until April, it is too late to initiate the separation of incoming recruits into the northern and southern fishery groups.

ENTRY OF RECRUITS INTO AREAS OF FISHERY

Fink and Bayliff (1970) discussed the migration of skipjack in the inshore areas of the eastern Pacific based on tagging experiments from 1952 to 1964 (Figure 2). The data are substantial for the immediate coastal areas of the fishery but much less so for the offshore island areas. In the northern fishery (Figure 2A) the principal entry point for small fish is the Revillagigedo Islands (lat 19°N, long 111°W) in April, and from there they move inshore from about May to June. In the southern fishery (Figure 2B) the situation is more complicated, but the entry of small fish only appears confirmed for the northern Panama Bight in April (and also into the Gulf of Guayaquil).

In view of the indications of size-specific movements through certain areas of the eastern Pacific fishery (Rothschild, 1965), the skipjack length-frequency data of the Inter-American Tuna Commission (IATTC) for 1954-1967 were reexamined, albeit subjectively, to obtain possible information on time of entry of young fish. Size range in the eastern Pacific fishery is about 36-74 cm, but more usually 42-62 cm. [Eastern Pacific length data from the U.S. fleet are selective because of the California minimum



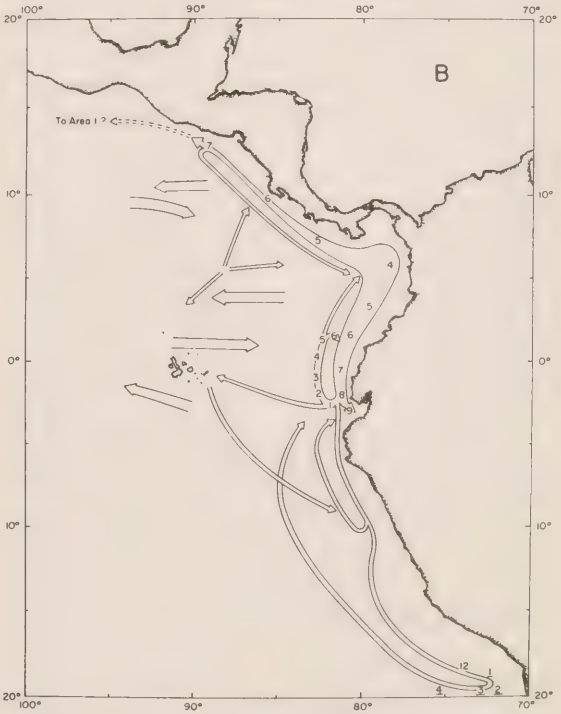


FIGURE 2.—Inshore migration of skipjack of the (A) northern fishery group (from Fink and Bayliff, 1970, Figure 89) and (B) southern fishery group (from Fink and Bayliff, 1970, Figure 90) based on tagging data; numbers refer to months.

landing size of 4½ lb (≈45-50 cm), but in South American landings by local boats (Manta) the smallest fish are about 36 cm.]

The length-frequency data in general show that the smallest skipjack in the northern fishery are found offshore at the Revillagigedo Islands from March to June. The modal size of these fish is <50 cm, and often between 40 and 45 cm. From March to May some similar sized fish are also seen in catches from adjacent inshore areas between the southern Gulf of California and Cape Corrientes (lat 25° to 20°N). Most of these small fish subsequently migrate into the skipjack fishery off western Baja California. In October (± 1 month) of most years there appears to be a small entry of fish, modal length ≤45 cm, at the Revillagigedo Islands, which is often reflected in the length-frequency distributions for November in the Baja California area.

In the offshore areas of the southern fishery a main influx of small fish, modal lengths <50 cm, appears to be at the Galapagos Islands from November to April with the peak in January and February. Data from the adjacent inshore area off Ecuador subsequently seems to reflect this entry of small fish. In addition, small numbers of skipjack of modal lengths ≤45 cm often occur in August (± 1 month) off Ecuador, as well as in Peru-northern Chile catches in abnormally warm oceanographic years. In the Cocos Island area fish of modal lengths ≤45 cm are found in January and February (there is some evidence this entry of small fish starts in November or December and lasts into March). Fish in this same size range subsequently occur in some years in the Gulf of Panama from April to June.

The apparent times and places of entry of small skipjack into the eastern Pacific fisheries are summarized below:

Fishery	*Area of entry*	*Time of entry*
Northern	Revillagigedo Is.	March-June October (± 1 month)
Southern	Ecuador	August (± 1 month)
	? Galapagos Is.	
	Galapagos Is.	November-April (peak January-February)
	Cocos Is.	November-March (peak January-February)

These findings are generally consistent with those of Fink and Bayliff (1970) for the northern fishery and expand those for the southern fishery.

Work on the growth of central-east Pacific skipjack using length-frequencies has been complicated by the problem of size-specific movements through the fisheries. Additionally, there is as yet no secondary age estimation method for the species. Recent work by Yoshida (1971), on young skipjack from the stomachs of longline-caught billfish in the central Pacific, has indicated that a 1-year-old skipjack may be about 31 cm. This is a similar length to that deduced from tagging data (averaged) for eastern Pacific fish by Joseph and Calkins (1969), who discuss the various deduced growth rates for the species, whereas Rothschild (1967), on the basis of short-term tag returns, indicated about 44 cm for a 1-year-old fish. Depending on the accepted growth rates, recruits to the eastern Pacific fisheries might thus be between 8 and 15 or 12 and 24 months old on entry and between 15 and 24 or 24 and 36 months old when departing the region for first spawning in the central Pacific.

CIRCULATION IN THE EASTERN TROPICAL PACIFIC

The oceanography of the eastern equatorial Pacific was reviewed by Wyrtki (1966, 1967). The circulation of intertropical surface waters shows the west-flowing North and South Equatorial Currents (NEC, SEC) with between them the relatively narrow (180-360 miles) east-flowing North Equatorial Countercurrent (NECC) at about lat 5°-10°N (Figure 3). At or just south of the equator below a depth of 20-50 m is the Equatorial Undercurrent (EUC) (Cromwell Current) with eastward flow.

However, Wyrtki (1965, 1966) indicated marked seasonal fluctuations in surface currents in the eastern Pacific. From June to December the NECC is fully developed through to the central American coast, while during January and May it is intermittent, and from February to

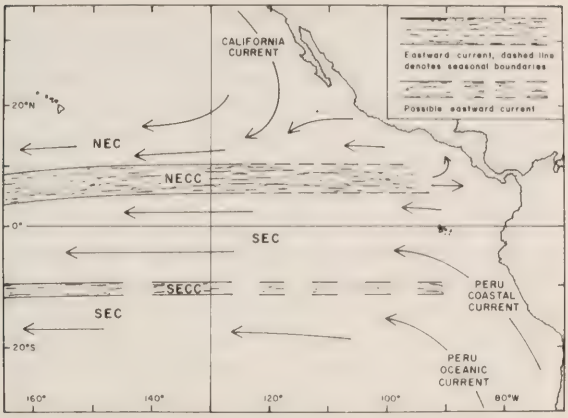


FIGURE 3.—Schematic chart of surface circulation in the tropical central-east Pacific Ocean. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.

April absent, east of long 120°W. Although Tsuchiya (1968) showed that below a depth of 50-100 m the NECC eastward transport is continuous throughout the year, more recent calculations of geostrophic flow from EASTROPAC data (M. Tsuchiya, unpublished data and personal communication) show that the subsurface transport is separate (deeper and slightly farther south) and that the surface NECC does cease or become minute and variable from January to May.

A striking relationship between development of the surface NECC and the latitudinal position of the Intertropical Convergence Zone (ITCZ) (meteorological equator) at the meridian of 120°W was presented in Wyrtki (1965). The NECC ceases east of long 120°W with the annual movement of the ITCZ south of lat 8°N about January, and when it returns north of lat 8°N about May, the NECC is reestablished. Hence, variations in the ITCZ position at long 120°W may be reflected in the time of cessation and resumption of the surface NECC, i.e., duration of the interruption. Abrupt interruption of the current is apparently not the case, and at least in January and May, it is weak and intermittent, and eddies and meanders may occur. [Superimposed on the overall monthly trend is also variability due to short-term (daily) fluctuations in ITCZ position.] Monthly ITCZ positions at long 120°W and NECC position based on Wyrtki (1965, Figure 18) are reproduced here as Figure 4, together with ITCZ monthly positions based on a 77-year mean of observations from the National Weather Records Center and prepared by the Goddard Space Flight Center, NASA (Allison et al., 1969). The position of the ITCZ is controlled by the variations in the location and strength of the wind fields in the central-east Pacific, the northeast and southeast trades, and the pressure fields associated with them.

Wyrtki (1966) stated the California Current is strong and penetrates farthest south and contributes most of the water to the NEC in the period February to April. The California Current is weak and located north of lat 20°N from August to December while in January and May-July it shows intermediate positions and strengths.

Tsuchiya (1968, 1970) has reviewed the present scanty information on the zonally narrow

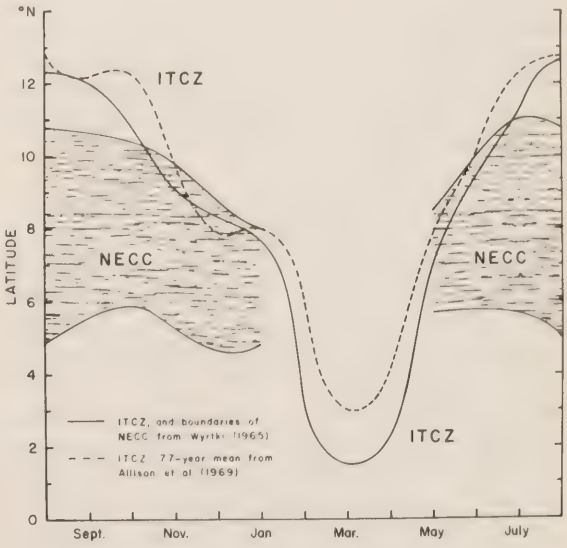


FIGURE 4.—Seasonal variations in the position of the Intertropical Convergence Zone (ITCZ) and of the boundaries of the North Equatorial Countercurrent (NECC) at long 120°W.

(2°-3° of latitude) South Equatorial Countercurrent (SECC), and shows that there appears to be a subsurface component at about lat 5°S. The surface SECC is ill-defined in the eastern Pacific (east of long 140°W) and M. Tsuchiya (personal communication) states that so far there is no physical oceanographic evidence from EASTROPAC data to confirm its existence.

FACTORS INFLUENCING SKIPJACK DISTRIBUTION

Blackburn (1965) considered that simple oceanic properties, such as temperature, directly determine overall limits of distribution of tunas, but that oceanic features and processes, among them surface currents, determine temporal and spatial differences in abundance within these limits. Though tuna distributions sometimes follow currents, he thought such relationships were often indirect, i.e., through property distributions associated with the currents. Blackburn was also of the opinion that the case for causal relationship between distribution of water masses and that of tuna species was inconclusive. However, Nakamura (1969) hypothesized that (i) tunas, according to species and life history stage, have their centers of distribution in distinct current systems or water masses, which provide specific habitats for them, and (ii) migrations of tunas are of two types, within a habitat and between habitats.

The consideration is now of the oceanographic factors influencing possible routes taken by skipjack when migrating from the central to the eastern Pacific. Throughout the tropical central-east Pacific near-surface temperatures are optimal for skipjack, except along the equator west of the Galapagos Islands out to long 100°W in certain months, and, of course, in the cold waters of the Peru Current. Given optimal temperatures, then the next factor governing distribution is probably the supply and distribution of food (Blackburn, 1965, 1969a, b). Adult skipjack are carnivorous on macrozooplankton and micronekton, and there is no reason to believe this does not hold for juvenile and adolescent skipjack, although the size range of the diet is probably smaller, that is more zooplankton. Even in adult fish Yuen (1959) for the Hawaiian Islands, Alverson (1963) for the eastern tropical Pacific, and Nakamura (1965) for the Marquesas and Tuamotu Islands presented evidence of smaller proportions of crustaceans and/or molluscs in large skipjack (over 60 cm) than in small ones. Contradictory evidence is found in the results of Waldron and King (1963), which showed no significant differences in the principal components of stomach contents of central Pacific skipjack.

Previous work in the equatorial central Pacific (Sette, 1955, 1956, and references therein; King and Hida, 1957; King, 1958; King and Iversen, 1962; Murphy and Shomura, 1972) indicates that there occur zonal "productivity" bands, representing various stages from nutrient enrichment to trophic levels, such as those represented by zooplankton and micronekton, which may be correlated with fish distribution. The principal such band normally exists between the southern edge of the NECC and a few degrees either side of the equator. Within this range there are latitudinal displacements of the "productivity" band (and its components) with time, probably as a function of the occurrence of the prevailing wind systems, the southeast and northeast trades (see Murphy and Shomura, 1972, for detailed discussion). A second, less intense[3] and more transient (or poorly documented) "productivity" band appears to exist close to the pycnocline at the NECC/NEC boundary. Its intermittent nature may be due to the nature of the mixing processes, such as ridging (Cromwell, 1958). Reid (1962) presented charts of average zooplankton volume (for upper 150 m) that indicated the existence of these two zonal bands in the central-east Pacific. In addition, he indicated a narrow zonal "productivity" band from lat 15°S in the east to about lat 10°S in the central Pacific. Close to the shore the zonal bands merged with features related to coastal distribution.

EASTROPAC zooplankton and micronekton data published in Atlas form (Love, 1970, and in preparation) in general confirm the existence of the northern and equatorial zonal "productiv-

[3] May be due to biased sampling procedures (Blackburn and Laurs, 1972; Maurice Blackburn, personal communication).

ity" bands in the eastern tropical Pacific. More detailed statistical treatment (for significance of interactions) of EASTROPAC primary productivity, phytoplankton, zooplankton, and micronekton data (Owen and Zeitzschel, 1970; Blackburn et al., 1970) from the western EASTROPAC area (lat 16°N-3°20'S, long 100°30'-121°30'W) show clearly the equatorial zonal band(s). However, the band at the NECC/NEC boundary is not clear at trophic levels other than zooplankton, and possible reasons for such anomalies are discussed in some detail. In addition, Owen and Zeitzschel (1970) pointed out that latitudinal effects may have been eliminated due to selection of geographic zones which do not coincide with natural (zonal) current systems.

Blackburn and Laurs (1972) have discussed the distribution of that part of the EASTROPAC micronekton catches which can be classified as skipjack forage. They not only confirm the existence of equatorial bands of high forage concentrations just north of the equator, and occasionally south of it, but also of a band at the NECC/NEC boundary, particularly in daytime catches.

There is some biological evidence from EASTROPAC data of increased "productivity"-zooplankton, micronekton, occurrence of birds (Love, 1970, and in preparation; R. M. Laurs, personal communication)—at certain times between lat 5° and 15°S, particularly lat 12°-14°S, the general region where the surface SECC might be expected. Such increased "productivity" could occur if a divergence existed in these latitudes, say at the southern SECC/SEC boundary.

Generally in the EASTROPAC area standing stocks decreased from east to west (Blackburn et al., 1970), that is from inshore to offshore, as did zooplankton in the charts of Reid (1962).

PROPOSED MIGRATION MODELS

ACTIVE MIGRATION MODEL (Figure 5)

Skipjack larvae are rare east of long 130°W (Matsumoto, 1966; Ueyanagi, 1969), and this generally appears to be borne out by the results of the EASTROPAC expedition (Love, 1970, 1971, and in preparation). It would seem, therefore, that adult skipjack spawn in the surface waters to the west of long 130°W, which in some way must be ecologically suitable for optimum survival and development of the larvae. In this model it is assumed that these larvae, and early juveniles, are maintained within the central Pacific by some passive migration system, perhaps related to the equatorial zonal current systems, eddies associated with island wakes, as well as diel vertical migrations.

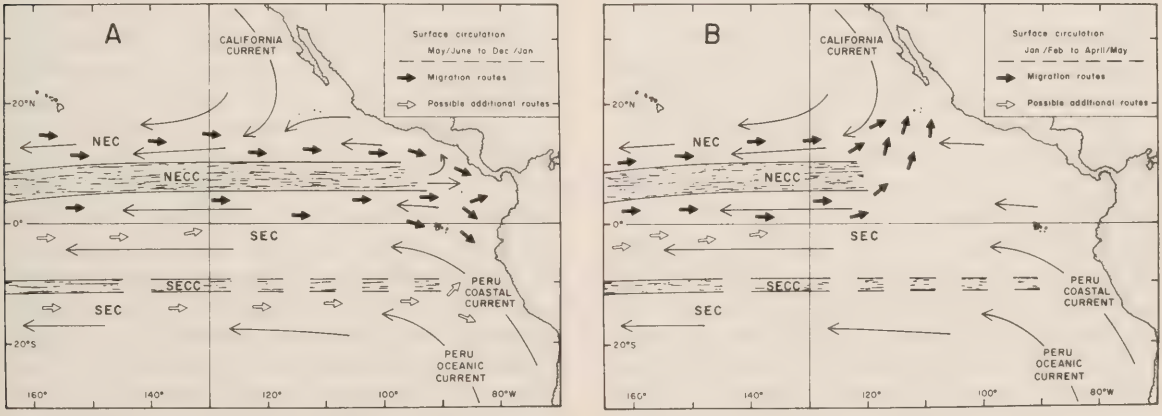


FIGURE 5.—Active migration model: (A) routes of young skipjack into the southern fishery and (B) routes of young skipjack into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Countercurrent; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.

At a certain size a large component of these juveniles start an active migration eastwards which ends with them on the feeding grounds of the northern and southern fisheries off the American continent. The size at which this active migration commences is not known, but with recruitment to the fisheries at 35-40 cm it is probably at <30 cm.

When in the eastern Pacific skipjack are feeding heavily, and this appears related to both the food requirements of the adolescent fish for normal growth and for the early development of the gonads. The departure of the fish with maturing gonads from the feeding grounds is attributed to a reproductive drive to return to the central Pacific where final maturation of the gonads and spawning must take place.

Richard S. Shomura and Richard A. Barkley (personal communications), with arguments based on central Pacific data, have suggested two spawning groups (northern and southern) are present in the central-east Pacific skipjack subpopulation(s) with considerable geographic overlap in equatorial areas. One group spawns during the northern summer, peak in July, and the other in the southern summer, peak in January. There is some slight evidence (Orange, 1961) that skipjack in the eastern Pacific fisheries are from two such spawning groups. Fujino (in press) has indicated that in the western Pacific subpopulation of skipjack there are two spawning groups (northern and southern) with a large overlap in geographic distribution.

Even though larval and early juvenile skipjack obviously make diel vertical migrations (Wade, 1951; Matsumoto, 1958; Strasburg, 1960; Ueyanagi, 1969, 1970; Higgins, 1970), the lower end of the temperature range is thought to be restricted to about 24°C, at least for larvae (Ueyanagi, 1969; Richards, 1969; Eric Forsbergh, personal communication). However, the adolescents arriving on the feeding grounds of the eastern Pacific fishery seem to have attained a physiological condition which permits them to exist at ambient temperatures down to 20°C, and occasionally 17°C, which are found in the near-surface waters of these zones (in other areas of the world, such as Tasmania, they may be as low as 15°C, Robins, 1952). Ability of skipjack to tolerate low ambient temperature (conserve internal heat) is probably a function of size (sequential physiological events), and this is also important in relation to the depth capability of the fish in its search for food at various life history stages. It is worth noting that skipjack have been shown (see below) to maintain body muscle temperatures considerably above ambient water temperatures:

Skipjack length (cm)	*Ambient water temperature (°C)*	*Body muscle temperature (°C) above ambient*	*Source*
43-47	25.6	8.5-9.1	Stevens and Fry (1971)
47-56	19.4-30.6	5-6	Barrett and Hester (1964)
71-76	26.6	4-8	Stevens and Fry (1971)
--	18.5, 29, 30	11.7, 7.8, 8.3	Carey et al. (1971)

Obviously the principal factors to be explained eventually in the the active migration model are those which induce the juvenile skipjack to migrate out of the central Pacific. Such a genetically fixed behavioral pattern undoubtedly would be a response to a summation of effects caused by exogenous and endogenous stimuli. Baggerman (1960) considered that migration, basically a function of locomotion and orientation, only occurs when fish are in the proper physiological condition and subject to external "releasing" factors (stimuli). This physiological condition, in turn, is brought about by endocrinal activity initiated by endogenous rhythms and external "priming" factors. This concept of causation of migration possibly may well apply in the case of tuna.

Hoar (1959) noted that for fishes with mass cyclical migrations at certain life history stages (such as reproduction, movement from nursery to feeding grounds) changes in endocrine secretions (gonadal, thyroidal) appear to play a major part in the generalized appetive behavior associated with migration. Woodhead (1959a, b) discussed the role of the thyroid in the migrations of mature and immature Barents Sea cod described by Trout (1957). It appeared that the "dummy run" contranatant migration of the im-

mature cod was under thyroid control, a distinct cycle in thyroid follicular cell height being observed although less than in mature fish. Woodhead (1959a) and Woodhead and Woodhead (1965) suggested production of such an active migration could be due to a general increase in swimming activity and in reaction to water currents (particularly a tendency to swim against them) caused by the increase in thyroid hormones. The thyroid in tuna, unlike most teleosts (including the cod), is a discrete bilobed structure (Honma, 1956—bluefin tuna; Williams, unpublished—skipjack and yellowfin tuna). If, as the juvenile skipjack approaches the size associated with first migration, the thyroid becomes more active and one effect of this is to initiate a similar behavioral response as in the cod (increased locomotor activity), then there would be a subsequent demand for more food if the growth of the animal is to be continued. At such time it is suggested that the increased food requirements—amount, type, size—cannot be supplied in the central Pacific near-surface waters, or that the young skipjack come increasingly into competition for the available food with other species and also their own adults. (See also discussion of evolution of migration patterns in Rothschild and Yong, 1970.) Additionally, the endocrine induced internal stimuli may also act to lower thresholds for recognition of changes in environmental conditions to the magnitude of those found in the equatorial central Pacific.

Sequences of events, such as mentioned above, could possibly trigger the active migration of juvenile skipjack out of the central Pacific—the main component being to the feeding grounds in the neritic eastern Pacific. It is proposed that the migrating skipjack juveniles are principally located in the equatorial areas of the west-flowing NEC and SEC. With near-surface temperatures optimal, except at the equator west of the Galapagos Islands at times of intense upwelling, the fish are located within or close to the equatorial and northern "productivity" bands described previously. In view of the apparent intermittent nature of the northern band, it is possible that the incidence of small, but frequent fronts may also act as concentrating mechanisms for food organisms normally observed at a low density in this area, lat 5°-10°N (Murphy and Shomura, 1972). Skipjack may also be associated with the possible "productivity" band around lat 10°-15°S.

The mechanisms which maintain the overall eastward orientation of the skipjack in an offshore oceanic area (in the absence of reference points) are unknown, although as Hoar (1953) commented "fish possess an elaborate and delicate array of highly specialized peripheral sense organs and appendages" and these could all be involved in some type of navigating ability in tuna. In this respect the probable role of the pineal apparatus of tunas as a photoreceptor (Rivas, 1953) should not be overlooked. Royce, Smith, and Hartt (1968) in a discussion of possible guidance mechanisms in oceanic migration models of Pacific salmon concluded that they may depend on electromagnetic cues from ocean currents and that responses to all migratory cues are inherited. Recent work by Yuen (1970) on tracking of small skipjack (with ultrasonic tags and continuous-transmission frequency-modulated sonar) moving on and off banks in the Hawaiian Islands lead him to imply that skipjack can navigate and have a sense of time.

It is hypothesized that incoming juvenile skipjack move continuously eastwards past the meridian of long 130°W, orientating largely to the zonal "productivity" bands (northern and equatorial) until entering the offshore areas of the southern fishery from August to April. However, the interruption or cessation of the surface NECC east of long 120°W in the period January-February to April-May might be expected to disrupt the orientation and movement of incoming skipjack juveniles, mainly through significant changes in the position or continuity of the "productivity" bands and food-concentrating mechanisms. It is at this period of the year that recruitment to the northern fishery is postulated.

Certainly the cessation of the NECC would cause the deepening of the mixed layer in the vicinity of the previous northern boundary of the NECC, and hence the elimination of possible ridging and subsequent increased biological productivity, though it is very difficult to estimate the lag period. In the case of the equatorial band (east of long 120°W) the annual southward

passage of the ITCZ causes a rapid change from predominantly southeast trades to either northeast trades or light easterly winds/doldrumlike conditions. In the former case, there would be divergence at the equator and formation of a weak convergence some distance south of the equator, while in the latter case there would be equatorial divergence but no convergences. Either way it would seem that there might be significant disruption of the "productivity" bands. However, EASTROPAC data do not show this very clearly, perhaps due to the lag period in the establishment of the higher trophic levels.

If a surface SECC is present in the eastern Pacific (even seasonally) then eastward movement of juvenile skipjack could possibly take place in the SEC near a southern "productivity" band (at the SECC/SEC southern boundary). Subsequently there would be an active migration of juveniles from near the SECC terminus into the southern fishery. However, water temperatures alone could prevent any direct recruitment from this area to the southern fishery during part of the southern winter. [In this and subsequent migration models speculations are not made on skipjack distribution south of the possible SECC/SEC southern boundary.]

Tuna have to swim continually to ensure ventilation across the gills and to maintain hydrostatic equilibrium, and maximum speeds in excess of 10 body lengths per second (bl/sec) have been reported (Blaxter, 1969, and references therein). For the closely related little tuna (*Euthynnus affinis*), Magnuson (1970) reported the minimum speed for hydrostatic equilibrium in a 42-cm fish was about 1.4 bl/sec and calculated for a 10-cm fish it would be about 3 bl/sec. After feeding, the average speed of the same captive fish increased to about 2 bl/sec, while Walters (1966) recorded for a 40-cm fish a speed of 5.9 bl/sec on a feeding run on dead fish and a maximum speed of 12.5 bl/sec. Magnuson (1970) also pointed out that the little tuna appears to spend most of its time swimming at speeds near the minimum hydrostatic speed and relatively little near the maximum. For captive skipjack of 38, 39, and 48 cm, John J. Magnuson (personal communication to Maurice Blackburn) indicated that the observed mean speed was about 2 bl/sec; for calculations for model fish the minimum speed for a 15-cm juvenile skipjack would be about 3 bl/sec. Actively migrating juvenile skipjack may be expected to have a narrow range of theoretical minimum speed, from 2 to 3 bl/sec.

The tracking of 40-42 cm skipjack in the Hawaiian Islands by Yuen (1970) showed that movement off a bank at night, principally from 1800 to 0200 hr, was mainly near the surface and without frequent directional changes, at speeds equivalent to about 1.5-6.0 bl/sec. However, during daylight, apparent speeds fell well below Magnuson's calculated minima which, Yuen concluded, must indicate considerable turning from a straight line track, presumably due to food searching and feeding—[skipjack are primarily daylight feeders (Nakamura, 1962)]. In addition, there was a greater variability in depth during the day than the night. On a recent cruise (Williams, 1971) small groups of skipjack were observed from the deck and underwater bow chamber swimming just ahead of the RV *David Starr Jordan* for considerable lengths of time. For the size of fish involved, a sample of four ranged from 60 to 64 cm FL, and the ship's trolling speed of 6½ knots, the skipjack were maintaining speeds of about 5.5 bl/sec.

In view of the above data it is considered reasonable to assume a mean swimming speed for incoming young skipjack equivalent to about 3 bl/sec "made good" in the direction of the oriented movement (migration) over the 24-hr period, i.e., about 50 miles per day. Hence, the first recruits entering the offshore areas of the southern fishery at the beginning of August may well have passed the meridian of 120°W about 6 weeks earlier, i.e., in mid-June shortly after the surface NECC is reestablished east of that meridian. Similarly, the last recruits to this fishery, in entering the offshore areas about the beginning of April, would have passed long 120°W about mid-February close to the time of, or shortly after, the interruption of the surface NECC east of that point. Thus, at the time of entry of the principal component of recruits from November to April, peak January and February, the surface NECC is established

east of long 120°W. It is considered that from February to April-May, when the surface NECC is absent east of long 120°W, the juvenile skipjack are being recruited to the northern fishery where they occur in the offshore area (the Revillagigedo Islands) from about March to May-June (arrival April-June onwards in Baja California). From long 120°W (lat 0°-10°N) about 2-4 weeks would be required for the skipjack to reach the Revillagigedo Islands, which agrees closely with the actual occurrence of juvenile skipjack at that location.

It will be recalled that one of the possible splitting mechanisms proposed by Rothschild (1965) was the >28°C surface water cell off Central America, but which it has been shown is not well developed out to long 120°W until April. Thus, even if >28°C water was limiting for skipjack (in quantity), and not >29°C water as shown recently (Williams, 1970), then that cell could not initiate the split as early as February.

The occurrence of small size fish at the Revillagigedo Islands in October (± 1 month) in some years is not accounted for in this model. This could occur if in midsummer some recruits destined for the southern fishery and located close to the northern boundary of the NECC (about lat 10°N) were deflected northward from their migration route by the >29°C water cell normally stretching southward from Central America at that time.

It is proposed that a gating or shunting mechanism operates at about long 120°W across the equatorial and northern migration routes of juvenile skipjack. When the NECC is continuous east of long 120°W, the gate is open and recruitment is to the southern fishery (Figure 5A). Then, with the annual southward movement of the ITCZ, the surface NECC ceases east of long 120°W, and the gate is closed from about February to April-May. Recruitment to the southern fishery ceases and instead the flow of recruits is to the northeast and into the northern fishery (Figure 5B). When the gate is closed there is a loss of west-east orientation due to changes consequent on the breakdown of the surface NECC, such as the loss of the current boundary conditions (with NEC and SEC), possible interruption (total and partial) of the zonal "productivity" bands, loss of food concentrating mechanisms (minor fronts), etc. The principal question then is how the recruit skipjack become oriented to the northeast, i.e., towards the Revillagigedo Islands. There could well be random dispersal of incoming recruits when the gate closes at long 120°W, with only a small proportion moving northeastwards into the California Current Extension and the majority eventually recycling to the central Pacific. Possibly those fish moving northeast pick up a "food bridge" linking the area around long 120°W in the vicinity of the NECC with the Revillagigedo Islands and Baja California. Such a "food bridge" could be provided offshore by the pelagic stages of the red crab (*Pleuroncodes planipes*) which are found in the California Current Extension (Longhurst, 1967, 1968; Longhurst and Seibert, 1971), the gradient of abundance of which increases towards the northeast (shorewards). It will be remembered that the California Current Extension is strongest and farthest to the southwest at this period. Red crab are known to form a large part of the diet of skipjack in Baja California waters during the fishing season (Alverson, 1963). A "food bridge" facilitating the northeast movement of recruit skipjack, because of survival value, may have become an inherited behavioral response when west-east orientation is lost around long 120°W in the period February to April-May.

One possible objection to the gating mechanism could concern efforts by the juvenile skipjack to dive below its effects. This is considered unlikely in view of adverse temperatures (<20°C) at depths where subsurface eastward flow is continuous and low oxygen concentrations at relatively shallow depths, at least as far south as lat 10°N. Oxygen content as low as 3 ml/liter has been suggested as possibly limiting for skipjack (Commercial Fisheries Review, 1965).

PASSIVE MIGRATION MODEL (Figure 6)

In this model it is hypothesized that larval and juvenile skipjack are passively carried eastward in the equatorial countercurrent(s) from the central Pacific spawning grounds to the offshore areas of the eastern Pacific fisheries.

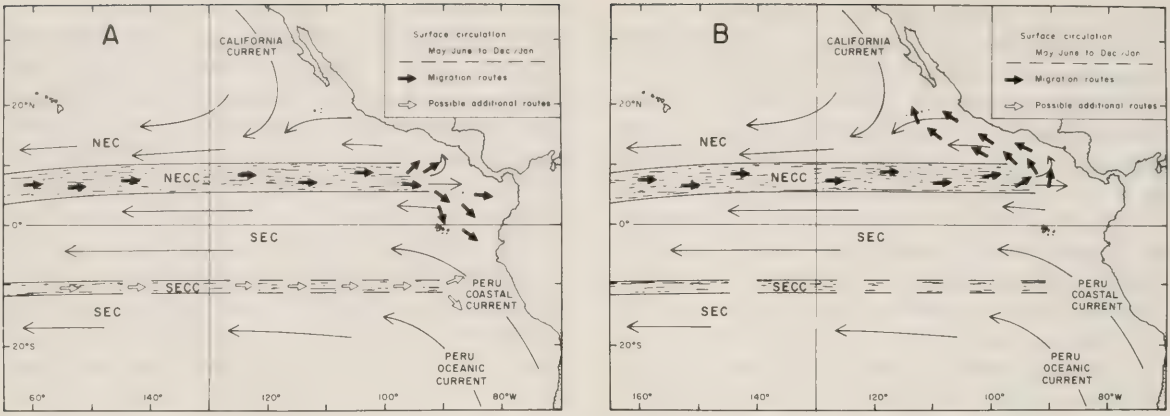


FIGURE 6.—Passive migration model: (A) routes of young skipjack into the southern fishery and (B) routes of young skipjack into the northern fishery. NEC = North Equatorial Current; NECC = North Equatorial Current; SEC = South Equatorial Current; SECC = South Equatorial Countercurrent.

Many of the larval and early juvenile skipjack in the central Pacific would originate in, or be involuntarily transported into, the NECC and while developing in this current (few larvae are found east of long 130°W) would be transported eastward with it. Although generally increasing in a west-east direction the productivity, in terms of zooplankton, of the NECC appears relatively low (Reid, 1962), though the incidence of small fronts in the NECC area (Murphy and Shomura, 1972) would be likely locations for aggregations of food organisms. The rapidly growing and increasingly active skipjack juveniles would need therefore to forage extensively for food and, in view of the large numbers involved, this may also necessitate foraging near the edges of the "productivity" bands at or close to the NECC boundaries (the net transport of the fish would necessarily be eastwards).

The concept of a passive migration eastwards with the NECC eliminates the otherwise difficult question of orientation in the young fish. The dispersion of juveniles from the NECC, at its nearshore terminus, to the southern fishery would be relatively simple and similar to that in the active migration model (Figure 6A). For recruitment to the northern fishery the problem is more complex, depending on whether the fish destined for that area are transported when the NECC flows through to the coast or when it is intermittent or stopped east of long 120°W.

The surface current system along the central American coast (Wyrtki, 1965), at least from May-June to December, is such that juveniles could be passively transported from the nearshore terminus of the NECC to the Revillagigedo Islands area (Figure 6B). However, from about April to September warmwater cells (>29°C) of varying sizes off Central America would prevent transport of the juveniles close to the coast and with increasing offshore distance the risk would increase of passive transport westwards into the NEC and not to the Revillagigedo Islands. With the principal influx of fish into the offshore areas of the northern fishery being from March to June, approach to these areas would need to be taking place in the first months of the year, and this is in fact the time when the coastal current system appears least likely to support such a passive migration. Thus, there are some real problems of timing with the passive migration of young skipjack into the northern fishery in the NECC and Central American coastal currents.

If recruitment to the northern fishery takes place after the cessation of the NECC east of long 120°W, then it would require an active migration from the terminus of the NECC to the

Revillagigedo Islands (as proposed in the active migration model at this time of year). In the period prior to cessation, when the NECC is intermittent, juvenile fish would increasingly lose their eastward orientation, some being deflected into the weak NEC and with a sufficient northward component in the current might passively reach the Revillagigedo Islands, though such conditions would be short-lived.

Should recruitment to the northern fishery not take place at the time of cessation of the NECC, juvenile skipjack at that time being recycled to the central Pacific in the NEC and SEC, then all recruits to the eastern Pacific fisheries would have to be carried to the coast in the NECC in the period May-June to December-January. From long 130°W (eastern limit of spawning area) to 85°W (approximate NECC nearshore terminus) is 2,700 nautical miles and with an average NECC speed of ¾ knot, continuous passive movement over this distance would take about 5 months. This would make the arrival time at long 85°W October-November to May-June. Obviously transport time could be much longer than this, if, for instance, (i) daylight hours were entirely spent foraging and with near-zero movement eastward, and/or (ii) real transport rates were lower due to the effects of diel vertical migrations. From the NECC terminus at about long 85°W recruitment, even passive, to the initial southern fishery areas would probably take no more than 4-6 weeks, i.e., arrival November-January to June-August. But a passive drift from the NECC terminus northwest to the Revillagigedo Islands with surface currents about ½ knot would take in the order of 4-5 months, i.e., arrival February-May to September-December. However, the recruitment size of the skipjack to both northern and southern fisheries appears similar. Several factors might be proposed to account for this fact: (i) the spawning grounds of the fish found in the southern fishery are farther west in the central Pacific than those of the northern fishery, (ii) the early life history stages enter the NECC at different sizes, (iii) behavioral patterns of the juveniles (from the two groups) in the NECC are different, or (iv) the juveniles stay longer in the offshore areas of the southern fishery than the northern one. Of these proposals the first seems most likely, and would be understandable if the two fishery groups did represent parts of two spawning groups (northern and southern) as suggested earlier (see page 748). One feature which could influence the eastern boundary of the groups spawning in the central Pacific, particularly the southern one, would be the westward extent of the influence of low near-surface temperatures at and south of the equator due to equatorial upwelling and effects of Peru Current water.

A wide degree of geographic overlap of the spawning groups in the central Pacific would alleviate problems of recruitment of young stages of southern spawners into the NECC, as trans-equatorial migration might not then be involved to any extent. In addition, the occurrence of a surface SECC would provide a possible mechanism by which young stages of southern spawners from south of the equator could be carried passively into the eastern Pacific. However, as previously stated, the existence of a surface SECC has not yet been confirmed in the eastern Pacific.

Thus, as our knowledge stands at the moment the NECC could be passively carrying juveniles of both spawning groups into the eastern Pacific fisheries but at different sizes.

GYRAL MIGRATION MODEL (Figure 7)

The two models described so far are based on the assumption that larval or juvenile fish migrate, passively or actively, out of the central Pacific to feed in coastal surface waters of the eastern Pacific and then subsequently return to the central Pacific for first spawning. Between spawnings the adult fish diffuse outwards from the central Pacific to feed but rarely reenter the adolescent feeding grounds.

Incidental longline catches of skipjack through 1967 (Miyake, 1968; Walter M. Matsumoto, personal communication) indicate the widespread distribution of the adults. According to Matsumoto there is some evidence that areas of high longline catch-per-unit-effort of skipjack in the central-east Pacific show seasonal shifts which tend to coincide with the direction of flow of the

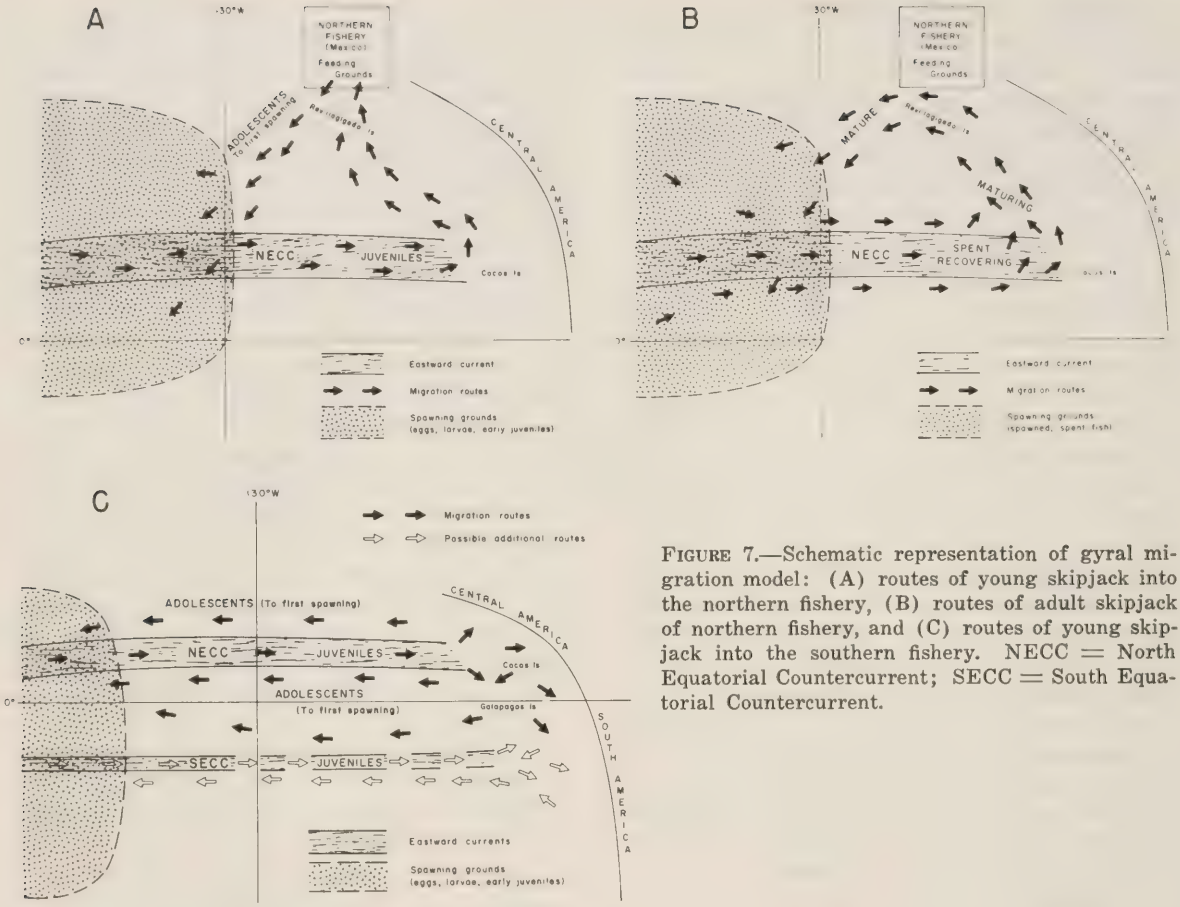


FIGURE 7.—Schematic representation of gyral migration model: (A) routes of young skipjack into the northern fishery, (B) routes of adult skipjack of northern fishery, and (C) routes of young skipjack into the southern fishery. NECC = North Equatorial Countercurrent; SECC = South Equatorial Countercurrent.

major ocean currents. Such movements appear to be counterclockwise in the southern hemisphere and clockwise in the northern hemisphere. The exception is in the eastern North Pacific where movement seems to be counterclockwise and corresponds to the narrow gyre of the northern equatorial water mass.

The above findings have suggested consideration of another type of model for skipjack, the gyral migration model, which involves all life history stages and both passive and active migrations. [Generalized gyral migration patterns are briefly discussed in Harden Jones (1968).]

For the northern fishery group it is proposed that the fish are moving counterclockwise around a zonally narrow equatorial gyre consisting of the NECC and the NEC, with the western limit some considerable distance west of long 130°W (possibly as far as long 170°W). In this model it is considered that mature skipjack spawn primarily in the northern spring-summer (May to October) in equatorial waters west of long 130°W, a large proportion of the subsequent larvae and early juveniles entering the NECC and with development then taking place in that current as proposed in the passive migration model (Figure 7A). The majority of the juveniles on reaching the terminus of the NECC are carried northwestwards with the coastal current off Central America, outside the warm-water cells >29°C. Movements of the adults would generally parallel the young stages, but they are in no way restricted to the NECC and may be found in a wide band covering the NECC

and adjacent areas of the NEC and the section of the SEC north of the equator (Figure 7B). This implies a navigational system in the adults. Thus, spent and spent-recovering fish would be expected in the areas immediately to the east of the spawning grounds. When the juveniles are off Central America and Mexico, the adults have also turned north and are located farther offshore and/or in deeper water. [It should be recalled that tag returns show little interchange of fish of the size caught in the eastern Pacific between the northern and southern fisheries (Fink and Bayliff, 1970).]

As the gyral group approaches the southern part of the northern fishery area, south and southeast of the Revillagigedo Islands, the juvenile skipjack actively migrate out of the gyre into the waters around the Revillagigedo Islands and subsequently into the feeding grounds off Baja California. The cue for the start of the active migration of the juveniles out of the gyre could involve a summation of external stimuli, such as those received on encountering California Current Extension (CCE) water, coupled with internal endocrinal stimuli, such as increased thyroidal and gonadal activity. Some adults migrate with the juveniles but the majority probably remain offshore. With the southerly advance of cold water (18°-21°C isotherms) along the west coast of Baja California in late fall, the adolescent skipjack leave the area of the northern fishery (Blackburn, 1969a; Fink and Bayliff, 1970; Williams, 1970). This they do via the CCE and rejoin the gyre, although no longer dependent on it for movement, the general transport of which is in a west-southwesterly direction (NEC). The adolescent skipjack, now maturing for the first time, and the adults thus return to the spawning grounds in the central Pacific in time for the next spawning season.

With regard to timing of movements in the gyre, the only real fact is that the principal recruitment to the offshore areas of the northern fishery, the Revillagigedo Islands, lasts from about March to June, with movement to Baja California waters normally from May onwards. A continuous passive migration of young stages from long 130°W to 85°W in the NECC and then to the Revillagigedo Islands in coastal currents might take about 9-10 months (see page 753). Backtracking from the entry time at the Revillagigedo Islands would suggest movement past the meridian of 130°W from about May-June to August-September. This is close to the suggested principal spawning season, May to October, west of that meridian for the northern spawning group. The adolescent skipjack leave offshore Baja California waters principally from November to January and, even if only moving at the speed of the current (CCE, then NEC), there is adequate time to reach the central Pacific west of long 130°W by spawning time.

The time between the proposed spawning period and first entry into the offshore areas of the northern fishery is about 10-12 months and might suggest that the higher of the growth rates mentioned earlier (see page 754) is the more likely in the first year, i.e., >40 cm. With a spawning period of May to October the proposed passive transport of juveniles east of long 130°W coincides with the period when the NECC flows through to the Central American coast. When the gyre is interrupted by the breakdown of the NECC east of long 120°W from February to April, there are probably no northern group young stages to be transported eastwards.

It is proposed that the skipjack forming the southern fishery group (from which the catch is usually much greater than that in the northern fishery) spawn principally in the southern spring and summer, November to April, in the central equatorial Pacific. A large proportion of the larvae and juveniles eventually enter the NECC where development ensues during the passive migration eastwards towards the American coast (Figure 7C). As with the northern group, movements of the southern group adults would parallel the juveniles in the NECC but would be primarily in the SEC. On reaching the terminus of the NECC, the juveniles migrate actively into the offshore areas, and subsequently the feeding areas, of the southern fishery off Central and South America (mainly off Ecuador). It is difficult to suggest a specific environmental cue which may act as the external stimulus involved in triggering this change from passive to active migration. Perhaps in the southern part of the area of the NECC terminus the cue could be

related to the waters of the Equatorial Front, especially those of Peru Current origin.

The adult skipjack at this period would normally remain offshore in the eastern Pacific. When the adolescents leave the feeding grounds they, and the adults, are maturing and would move westwards in the SEC (north and south of the equator), and possibly even in the NEC, to the central Pacific spawning grounds. There is some indication from the data of Miyake (1968) that maximum occurrence of longline caught skipjack was at about lat 10°-15°S east of long 105°W, at lat 5°-10°S from long 105° to 130°-140°W, and at lat 0°-5°S west of long 130°-140°W, that is tending towards the equator away from the coast. This could be related to equatorial low temperature areas west of the Galapagos Islands.

A principal problem with a gyral model for the southern fishery group concerns the entry of larvae and early juveniles into eastbound currents. For those originating in the equatorial areas of the NEC, or the SEC north of the equator, access to the NECC through known circulatory mechanisms is relatively simple (similar to that in the passive or northern gyral migration models). For larvae and early juveniles of this group south of the equator the problem is more complex. Here the SEC has a southerly component in the westward transport tending for passively drifting animals to be carried away from the equator. For those between lat 0° and 5°S a passive movement northwards and across the equator, and hence into the NEC, could occur under the stress of unusually strong southeast or south winds, the equatorial divergence then being farther south than usual.

This problem related to skipjack young stages south of the equator raises the question of the role of the SECC in the southern gyral migration model. Migration in the subsurface SECC is improbable as mean temperatures are about 14°C (M. Tsuchiya, personal communication). However, the existence of a surface SECC, even if as narrow as 120 miles, could be of importance in completing the gyre south of the equator (see Figure 7C). Larvae south of the equator in the central Pacific would tend to be carried towards the SEC/SECC boundary, and then eastwards with it. As mentioned earlier EASTROPAC and other data showed increased "productivity" in the general region where a surface SECC might be expected (lat 10°-15°S), and this would obviously be of importance in development of the juveniles. Subsequent movement of juveniles from the surface SECC terminus would presumably be in the form of an active migration. There could also be some type of link with the Peru Countercurrent. In the southern summer adolescent skipjack often occur off northern Chile and the north-south migration route of these fish must be offshore in view of the low coastal temperatures off Peru. Fish that migrated onshore in the SECC would move, after feeding off South America, westwards in the SEC and return to the central Pacific.

Obviously timing in the two gyral migration models would be different, even though they share a common eastbound current, the NECC. When this current is flowing through to the coast, it would carry recruit skipjack of two different sizes representing the two groups. Southern fishery group recruits would be considerably larger (4-5 months older) than those of the northern group. Separation of the juveniles of the two groups at the NECC terminus would be little problem as only those of southern group origin would be in the developmental physiological state requisite to active migration. Those juveniles belonging to the northern group would continue their passive migration. Intermingling of groups could occur if some northern group juveniles were passively carried into southern fishery areas especially off Central America.

As in the passive migration model (see page 753), to account for the size differences in incoming recruits, one would have to propose that: the southern group spawning grounds are farther west than those of the northern group, and/or the transfer mechanisms involved in the movement of young stages into eastbound currents are complex and take longer (certainly true if no SECC). Either or both of these proposals could account for southern group juveniles, spawned November to April, not reaching the area of long 130°W at the time when the NECC has stopped east of that meridian. Alternatively, if juveniles from the southern spawning group

(southern fishery group) were somehow retained west of long 130°W from February to April, when the NECC is stopped, then this would reduce the apparent distance westward from the coast that the entry times to the southern fishery would otherwise imply.

The existence of a surface SECC would certainly facilitate the recruitment of juvenile skipjack (of southern origin) into the southern fishery. However, one would expect such a current to be highly variable in space and time, and hence such recruitment would be similarly affected.

GENERAL COMMENTS AND RECENT RESEARCH

An active migration of juvenile skipjack from the central to the eastern Pacific would be categorized as a "between habitat migration," using the definition of Nakamura (1969). Similarly with the gyral migration models, the active migration of juveniles from the gyres to the feeding grounds would fit this definition. This type of migration, Nakamura suggested, takes place following a change in ecological state, for which one might perhaps synonomize developmental physiological state. Nakamura also hypothesized that "between habitat migrations," which entail changes in environment (current systems, water masses), occur principally at the equinoxes, about March in the northern hemisphere and September in the southern hemisphere, and that the movements are rapid and on a large scale. In the eastern Pacific the principal recruitment into the offshore areas of the northern fishery starts about March and lasts to about June; there is also some recruitment about October (± 1 month). However, recruitment to the offshore areas of the southern fishery appears to be over a considerably longer period, November to April, and perhaps from as early as August (± 1 month).

The Bureau of Commercial Fisheries (now the National Marine Fisheries Service), Honolulu, undertook five quarterly cruises, from May 1969 to May 1970, between lat 12°N and 3°30′S along the meridian of long 145°W, to consider the distribution and abundance of skipjack in the equatorial current systems. Preliminary data from these cruises (Walter M. Matsumoto, personal communication) show longline skipjack catches were generally low except in the area of the NECC (lat 7°30′N), where they were relatively high in the first and fourth quarters (February and October-November). Trolled catches of skipjack on the last three cruises were variable but consistently high in the NECC. Catches by both methods were lowest at the equator in the vicinity of the EUC. Catches of juvenile skipjack made with a midwater trawl were relatively high in the SEC at lat 3°30′S through most of the year, while catches in the NECC peaked in the second and third quarters (May and June). Plankton hauls (1-m net) showed largest catches of larvae were made in the SEC just south of the NECC.

These results suggest that skipjack north of the equator spawn in the second and third quarters, or even slightly earlier, and that the juveniles are concentrated in the NECC at this time. The high year-round abundance of juveniles at lat 3°30′S apparently indicates either sequential seasonal spawning of the northern and southern groups or continual equatorial spawning of a single group. Richard A. Barkley and Richard S. Shomura (personal communications) have previously suggested that the shallow EUC could be involved in the eastward transport of skipjack young stages. At least east of long 120°W this seems unlikely as even in the upper regions of the EUC temperatures (18°-20°C) are marginal for adult skipjack let alone larvae. Even in the vicinity of the EUC at long 145°W, where temperatures may be about 20°C, the lack of juveniles and adults would appear to confirm this finding.

Hida (1970) reported on an exploratory fishing cruise for tuna made by the Bureau of Commercial Fisheries, Honolulu, in October-November 1969 concentrated in the area, lat 6°N-8°S, long 115°-125°W. Surface schools of tuna fishable by pole-and-line were found from lat 2°-5°N (just south of the NECC); skipjack predominated in the catches, though some large schools consisted of yellowfin, bigeye, or all three mixed. The skipjack, caught by this method and trolling, ranged from 45 to 79 cm FL (means 47-68 cm) and gonads were maturing or mature (only one

spent). Only one school of small skipjack was fished by pole-and-line, at lat 4°S, and the fish were from 36 to 51 cm (mean 40 cm). However, enroute to and from Hawaii (lat 10°N-5°S, long 125°-145°W) troll catches of skipjack were mainly of small fish, <45 cm. The data from this cruise add little to the proposed migration models except to indicate the wide geographic range of recruit size skipjack west of long 125°W in October-November 1969. In addition, east of long 125°W fish were in the medium to large category and in schools large enough to be fished successfully by a commercial method—live bait pole-and-line. None of these fish had recently spawned.

Williams (1971) described plans for a series of eight cruises, initiated by the NMFS, La Jolla, and the Scripps Tuna Oceanography Research (STOR) Program, to investigate the distribution of skipjack in relation to environmental conditions in two offshore areas of the eastern Pacific. The two areas, (A) lat 15°N-5°S, long 115°-125°W, and (B) lat 5°N-15°S, long 95°-115°W, were considered the most important for testing migration models for skipjack, including the three now proposed for recruits.

The first cruise (two vessels) was to Area A in October-December 1970, with trolling as the principal fishing method. Recruit size fish ($\leqslant$40 cm) were found in the NEC some distance to the north of the NECC, as well as immediately to the north and south of the NECC. Large fish were widely distributed, but with fewest found in the NECC and most in the section of the SEC north of the equator. About 27% of the fish $\geqslant$45 cm, the gonads of which were examined, were found to be in a spent or spent-recovering condition; most were found in or close to the NECC, and none south of the equator. A first sorting of midwater trawl samples showed no skipjack juveniles; data on occurrence of larvae are not yet available.

The second cruise to the same area, in March-April 1971, caught few small fish and none <40 cm. More large fish were caught north of the equator than on the previous cruise. The presence of a surface NECC, even though weak and narrow (180-120 miles wide), at this time of year and at this meridian was anomalous. About 60% of the fish examined had gonads in a recovering state and were from all current systems north of the equator.

The results of these two cruises confirm that some skipjack spawn in the equatorial zone not too distant from long 120°W. Those fish taken in March-April 1971 appeared to have gonads in a more advanced state of recovery than most taken in October-December 1970 (subjective analysis). Presence of these spent and spent-recovering fish could indicate support for the gyral migration models, where it is proposed that after spawning west of long 130°W adults move eastwards paralleling the movement of the young stages. However, even with the active and passive migration models there could be small-scale diffusion movements of adults out of the central Pacific (including east of long 130°W) subsequent to spawning. The appearance of spent and spent-recovering gonads in October-December skipjack suggests they were of northern summer spawning origin, while the recovering gonads in March-April fish rather indicate southern summer spawners; or alternatively that spawning in skipjack is truly a year-round function in the equatorial zone. The apparent absence of juveniles in the trawl hauls may be due to ineffective sampling gear. The presence of very small fish (<40 cm) in areas of high forage concentrations at the NECC boundaries, as well as in the NEC somewhat further north, would tend to support the active migration models. They could be either some of the last recruits destined for the southern fishery or early ones for the northern fishery; their presence in the NEC as far north as lat 13°N, and size (30-40 cm) suggests the latter. The significance of the shift in the center of apparent abundance of large fish from lat 1°-5°N to 9°-11°N between October-December and March-April is not yet apparent.

A further six cruises, starting with one to the southern area (B) in August-October 1971, are planned. Data from this series of cruises will undoubtedly increase our ability to describe, particularly for offshore areas, the distribution, apparent abundance, life history, and environment of the skipjack. Although input of these data will be valuable in preparing models, such as

those of migrations, there is also a need for a greater input related to the physiology, behavior, and genetics of the species than is presently available.

The hypothetical nature of certain aspects of the proposed models of skipjack migrations advanced here cannot be denied. However, at this stage in the development of research on the skipjack resources of the central-east Pacific, a presentation of existing data and ideas on skipjack migrations, in the form of models, appears fully justified. Indeed present research plans were formulated on the basis of the active migration model (the first proposed), although they are equally applicable to testing the other models as well.

With any of the proposed migration models it is obvious that oceanographic conditions in the central-east Pacific will have a vital controlling effect on the subsequent abundance of skipjack in the eastern Pacific fishery. First, through year-class strength of recruits (spawning success/larval survival) and second, through the number of recruits actually entering the fishery (migration success). Not only is it necessary to test the mechanisms of these, and other, migration models, but monitoring and more detailed analyses of inter- and intraseasonal fluctuations in the central-east Pacific environment will assist in understanding, and perhaps in predicting, the fishery-independent changes in skipjack apparent abundance.

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HAWAIIAN-CAUGHT SKIPJACK TUNA AND THEIR PHYSICAL ENVIRONMENT

GUNTER R. SECKEL[1]

ABSTRACT

Empirical associations between the occurrence of skipjack tuna (*Katsuwonus pelamis*) in Hawaiian waters and environmental conditions point to the current system as an important cause for the variations in the Hawaiian fishery. Large interyear differences of sea-air interactions in the skipjack spawning areas may affect larval survival and year-class strength. A numerical drift model was used to investigate the contribution of currents to the travel of skipjack from the eastern North Pacific to Hawaii. Floating objects introduced in the model ocean at long 120°W and lat 10° to 20°N converge toward the northern edge of the North Equatorial Current near Hawaii in 21 to 23 months. The time of freedom of skipjack tagged in the eastern North Pacific and recovered in Hawaiian waters is of the same magnitude. It is concluded that for skipjack a possible mode of travel from the eastern North Pacific to Hawaii is drifting in the North Equatorial Current. The variability in abundance and size-frequency distributions observed in the Hawaiian fishery can be caused by changes in the current system. Numerical models of the type presented can be verified and so permit progress from the exploratory to the experimental phase in fisheries investigations.

Over a decade ago empirical associations were established between environmental parameters and the availability of skipjack tuna (*Katsuwonus pelamis*) to the Hawaiian fishery. Since that time oceanographic studies have provided additional information to augment these associations that can now be used to postulate causal relationships. Such hypotheses are an essential step in bringing ecological studies from the exploratory to the experimental phase, numerical analysis, and, eventually, prediction.

In this paper I will briefly review the empirical associations that were established and introduce new information that has resulted from the Trade Wind Zone Oceanography investigation. The empirical associations lead to two environmental processes that must be included in numerical models describing the distribution of skipjack. One concerns the sea-air interaction processes that may affect productivity and larval survival, and the other concerns the current field that affects the distribution of skipjack schools. The latter is illustrated by a numerical "drift model" for a portion of the Pacific North Equatorial Current.

The purely physical explanations that are given for the varying availability of skipjack in the Hawaiian fishery and the implications of the drift model results may conflict with beliefs based on biological considerations. Such conflicts can be resolved if the proposed hypotheses are tested experimentally as suggested in this paper.

It is fitting that this work should be reported in Dr. Sette's Festschrift. He provided great impetus and leadership to the integration of environmental studies with fisheries research. The work on Hawaiian-caught skipjack and on their environment was initiated at the time Dr. Sette directed the Pacific Oceanic Fishery Investigations (POFI) in Hawaii.

REVIEW OF EMPIRICAL ASSOCIATIONS

THE HAWAIIAN SKIPJACK FISHERY

The Hawaiian skipjack fishery has been described by Yamashita (1958) and Uchida

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(1966). Landings from this fishery range from about 91 tons[2] (200,000 lb) per month in February to more than 907 tons (2 million lb) per month in July. Total annual landings also show wide variations ranging from 2,676 tons (5.9 million lb) as in 1969 to 7,302 tons (16.1 million lb) as in 1965.[3] Hawaiian fishing vessels fish within sight of land, mainly in the vicinity of the islands of Oahu to Maui and Hawaii (Uchida, 1970). Thus, Hawaiian skipjack landings provide, in contrast to other fisheries where fishing fleets may follow the fish concentrations, a time sequence measure from a fixed area.

Uchida (1967) analyzed the catch and effort in the Hawaiian fishery and found that although there has been a decline in the number of vessels fishing on a full-time basis during the last 15 years, there is no clear evidence that this decline has affected total landings. It appears that the decline in the number of fishing vessels occurred primarily among the smaller boats (Uchida 1966: Table 6) and, also, that the decline was offset by increased efficiency of fishing. For purposes of this paper, it is important to note that the large fluctuations in total annual landings are also reflected by the average annual catch per standard effective trip (Uchida, 1967: Figure 8). The annual landings of skipjack, therefore, reflect availability near Hawaii.

THE OCEAN ENVIRONMENT NEAR HAWAII

The oceanographic climate of the Hawaiian Islands region was described by Seckel (1962). Of interest are the North Pacific Central and the North Pacific Equatorial water types and the transition water of the California Current Extension between these water types (Figure 1). Seckel (1968) defined the North Pacific Central water as that with a salinity of more than 34.8‰ and the North Pacific Equatorial water as that with a salinity of less than 34.2‰. These salinities are always found in the salinity gradients that actually define the water type boundaries.

The boundary of the North Pacific Central water lies near the Hawaiian fishing area and is displaced north-southward both seasonally and nonseasonally. Usually the boundary lies just south of the islands in fall and winter and within or north of the islands during spring and summer. The boundary displacement is reflected by the salinity as measured at Koko Head, Oahu (Seckel and Yong, 1971). Low salinities occur during spring and summer and high salinities during fall and winter. During some years, such as in 1957 and 1958, the islands were bathed in North Pacific Central water throughout the year and in 1968 the islands were bathed in the transition water of the California Current Extension throughout the year.

The large effect of heat exchange across the sea surface tends to obscure the effect of advection on the sea-surface temperature. Nevertheless, the change of temperature due to advection is apparent in graphs of the change of temperature per month (Seckel, 1962). Warm advection in late winter and early spring causes the temperature in Hawaiian waters to rise before it would rise due to the onset of seasonal heating across the sea surface. The temperature increases and the salinity decreases southward near Hawaii. Warm advection is therefore associated with a northward component of flow that also causes a decline in the salinity.

Extremes of temperature and salinity as observed at Koko Head, Oahu, range from about 22.5°C in February or March to 27.4°C in September or October and from 34.4‰ in July to 35.5‰ in late fall or early winter. Inorganic phosphate concentrations in the Hawaiian region as well as in the North Equatorial Current are about 0.3 μg at./liter. Seasonal variations have not been observed.

In the Hawaiian region 10 to 40 cc of zooplankton per 1,000 m^3 of water are filtered by a 1-m net in 200-m oblique tows (King and Hida, 1954, 1957a, 1957b; Nakamura, 1967). King and Hida (1954: Figure 16) indicate that an average zooplankton volume of about 25 cc per 1,000 m^3 of water filtered near Hawaii compares with 20 to 25 cc in the North Equatorial Current and with about 38 cc near the equator to the south of Hawaii. There is no clear indication of a sea-

[2] Metric tons are used throughout this paper.
[3] Source: Hawaii State, Division of Fish and Game.

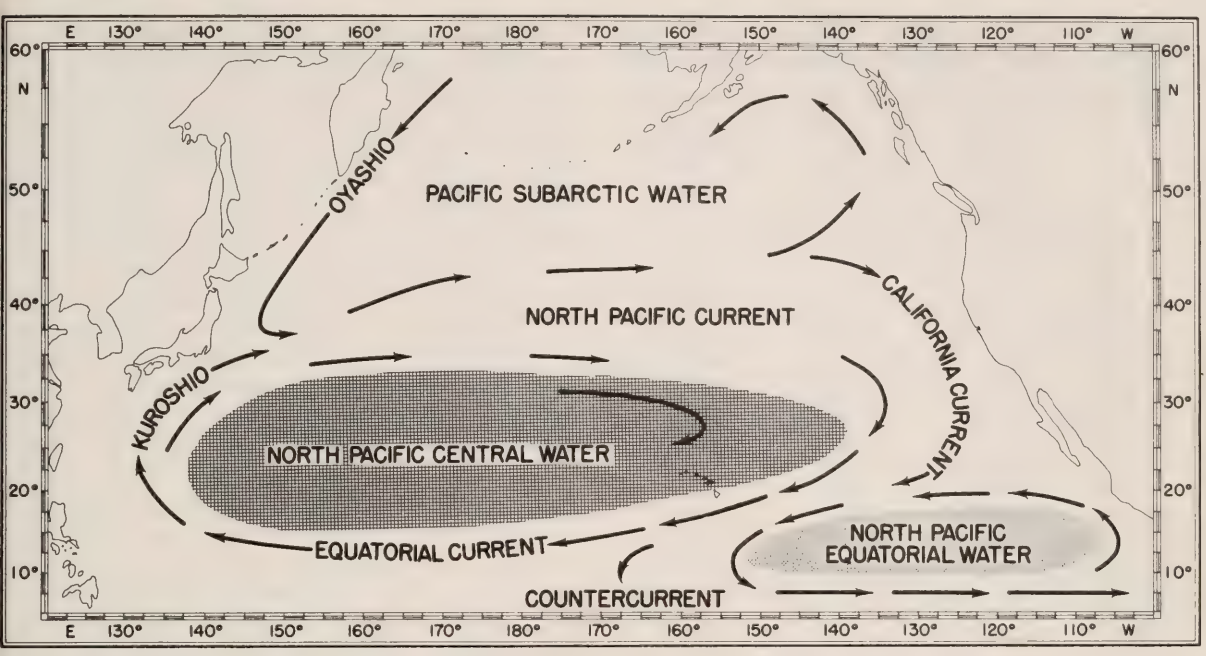

FIGURE 1.—Schematic chart of the major North Pacific water types and currents.

sonal variation in zooplankton concentrations in Hawaiian waters but longer term variations appear to take place. There has been no systematic sampling of tuna forage by midwater trawls.

SKIPJACK AND THE ENVIRONMENT

Blackburn (1965) summarized the range of environmental conditions within which skipjack are known to exist. The conditions summarized in the previous section fall well within this range. The seasonal changes in the Hawaiian environment are therefore not the probable cause for the variations in skipjack availability. Inorganic phosphates, as possibly affecting primary productivity, or the concentration of zooplankton vary insufficiently to explain a tenfold increase in catch rates during the summer months.

It is common to think of temperature and salinity changes in terms of their physiological effect on the biota. These changes, however, also reflect dynamic properties of the environment such as heat exchange across the sea surface and advection that, in turn, affect biological distributions. Thus, when temperature and salinity changes were used in the Hawaiian region as indices of heat exchange and advection (Seckel, 1962) associations between the dynamic properties of the environment and the availability of skipjack became apparent. Development of the empirical associations and their implications can be traced in Seckel and Waldron (1960), Murphy, Waldron, and Seckel (1960), Seckel (1962), U.S. Bureau of Commercial Fisheries (1963).

It was found that the seasonal intrusion of the California Current Extension water into the Hawaiian region, as reflected by the surface salinity, coincides with the seasonal increase in the availability of skipjack. To monitor this association, the salinity measured at Koko Head, Oahu, during July can be used as an index of the water type during the peak of the fishing season.

The northward component of flow during late winter and early spring that causes the displacement of North Pacific Central water by California Current Extension water near Hawaii, also causes warm advection. It was found that strong or early warm advection as reflected by

TABLE 1.—Annual landings of skipjack in Hawaii, 1952-1970, with time of initial warming and mean July salinities of sea-surface water.

Year	Time of initial warming[1]	July mean salinity (‰)[1]	Total landings 10^3 metric tons
1952	March	>34.8	3.31
1953	February	<34.8	5.47
1954	February	<34.8	6.36
1955	March	<34.8	4.40
1956	February	34.72	5.05
1957	March	34.98	2.78
1958	March	34.87	3.10
1959	February	34.73	5.63
1960	March	34.69	3.34
1961	February	34.77	4.94
1962	March	34.86	4.27
1963	February	34.84	3.67
1964	March	34.82	4.09
1965	February	34.67	7.33
1966	March	35.01	4.26
1967	January	34.83	3.65
1968	January	34.50	4.23
1969	February	34.72	2.71
1970	March	34.98	3.33

[1] Time of warming and July salinities are based on observations at Koko Head, Oahu, except 1952 to 1955 when they are based on observations irregularly made in the vicinity of Oahu.

initial warming occurring before the end of February precedes favorable fishing conditions. Weak or late warm advection is reflected by initial warming in March and precedes unfavorable fishing conditions.

The empirical associations are summarized in Table 1, giving the time of initial warming (temperature index), the mean July salinity, and the annual landings of skipjack in Hawaii. The indices are based on measurement, regularly made at Koko Head, Oahu, since November 1955. Indices between 1952 and 1955 are estimates based on sea-surface temperature and salinity observations irregularly made in the vicinity of Oahu. Prior to 1952 there were insufficient data to make estimates.

When the associations between availability of skipjack and time of initial warming were first established, monthly mean temperatures were used. Now Koko Head temperatures are expressed by harmonic functions of time (Seckel and Yong, 1971). These functions have been used to determine objectively the time of initial warming given in Table 1. Formerly, a salinity of 35‰ was used to indicate the boundary between North Pacific Central and California Current Extension waters. Here, in keeping with the definitions given by Seckel (1968), a salinity of 34.8‰ has been used to indicate this boundary.

The temperature and salinity indices can each be assigned a rating of favorable (F) or unfavorable (U) for fishing. There are therefore three categories according to which the landings are classified and shown in Figure 2a: Both indices favorable (FF), one unfavorable (FU or UF), and both unfavorable (UU).

The 1968 and 1969 landings did not fall within the FF range of previous years. Examination of environmental conditions revealed that during these years minimum salinities were the lowest recorded since the sampling series began at Koko Head, Oahu (Seckel and Yong, 1971). A sharp drop in values took place in late winter 1968 and the salinity remained low until late summer of 1969 when values rose to a normal level. Minimum salinities occurred in June 1968 and May 1969 and averaged 34.49‰ and 34.59‰, respectively. This information, as well as that to be introduced in the next section, indicates that favorable "skipjack water" is confined to the high-salinity portion of the California Current Extension. For favorable fishing conditions, therefore, the additional constraint is introduced that mean monthly salinities during spring must be above 34.6‰. With this new constraint, landings for 1968 and 1969 fall into the FU category (Figure 2b).

Of the 19 years for which skipjack landings in Hawaii can be associated with environmental conditions, 6 years fall in the FF category, 7 in the UU category, and 6 in the FU category when the revised salinity index is used. Figure 2b illustrates that there is a clear separation between the landings in the FF category on the one hand and the FU and UU categories on the other. The average annual landings are 5,800 tons, and 3,700 tons and 3,600 tons in the FF, FU, and UU categories, respectively. The lowest value in the FF category (4,900 tons) is higher than the highest value in the FU category (4,400 tons) or in the UU category (4,300 tons). The 19-year average of annual landings was 4,300 tons.

Annual landings, therefore, can be classified into two groups. One group comprises the landings in the FU and UU categories that average 3,600 tons and range from 2,710 to 4,400

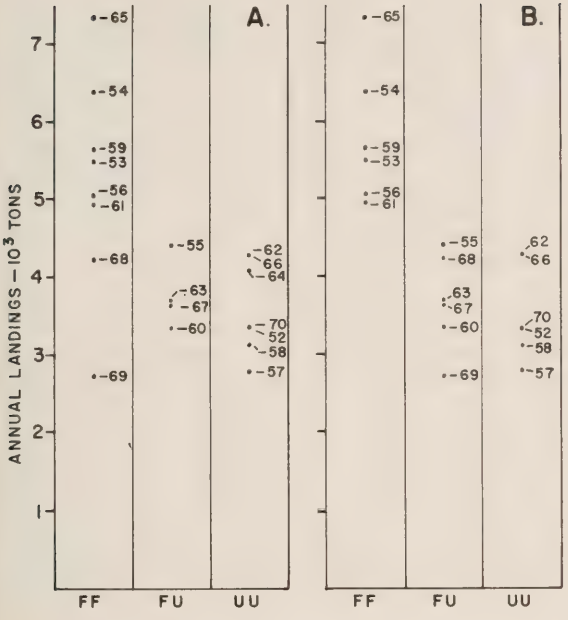

FIGURE 2.—Annual skipjack landings in Hawaii grouped according to the temperature and salinity indices being both favorable, FF, one favorable and the other unfavorable, FU, and both unfavorable, UU. Panel A: Salinity index is favorable with July salinity less than 34.8‰. Panel B: Salinity index is favorable with July salinity less than 34.8‰ but spring salinity higher than 34.6‰.

tons. The other group comprises the landings in the FF category that average 5,800 tons and range from 4,940 to 7,330 tons. Landings in the first group occur two-thirds of the time and are normal for Hawaii. Landings in the latter group are clearly exceptional.

Into which of the two groups landings will fall is in part predictable. The temperature index is determined in April, well before the beginning of the summer fishing season. The salinity, however, is monitored during spring and has little predictive value. During the 19 years under consideration there have been 4 years when the temperature index was favorable but the salinity was unfavorable. Two of these years were 1968 and 1969, when the spring salinity was the lowest recorded at Koko Head. Thus, the temperature index can be used to predict the exceptional fishing years in four out of five cases. This predictability can be improved by subjective interpretation of the salinity trends prior to the fishing season.

SKIPJACK AND THE TRADE WIND ZONE OCEANOGRAPHY RESULTS

In the Trade Wind Zone Oceanography (TWZO) investigation, oceanographic stations were occupied at fixed locations between lat 10° and 26.5°N along long 148°, 151°, 154°, and 157°W at approximately monthly intervals from February 1964 to June 1965 (Figure 3). Although

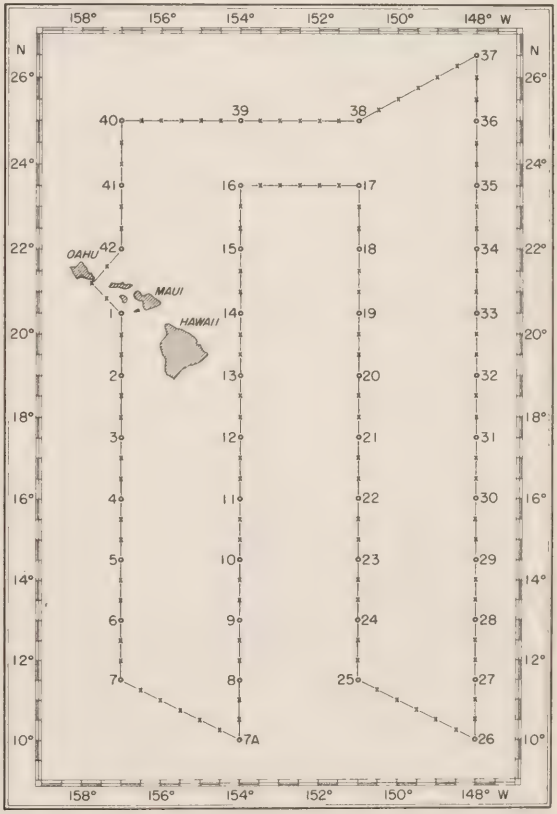

FIGURE 3.—Track of the Trade Wind Zone Oceanography cruises. Numbered circles indicate oceanographic stations.

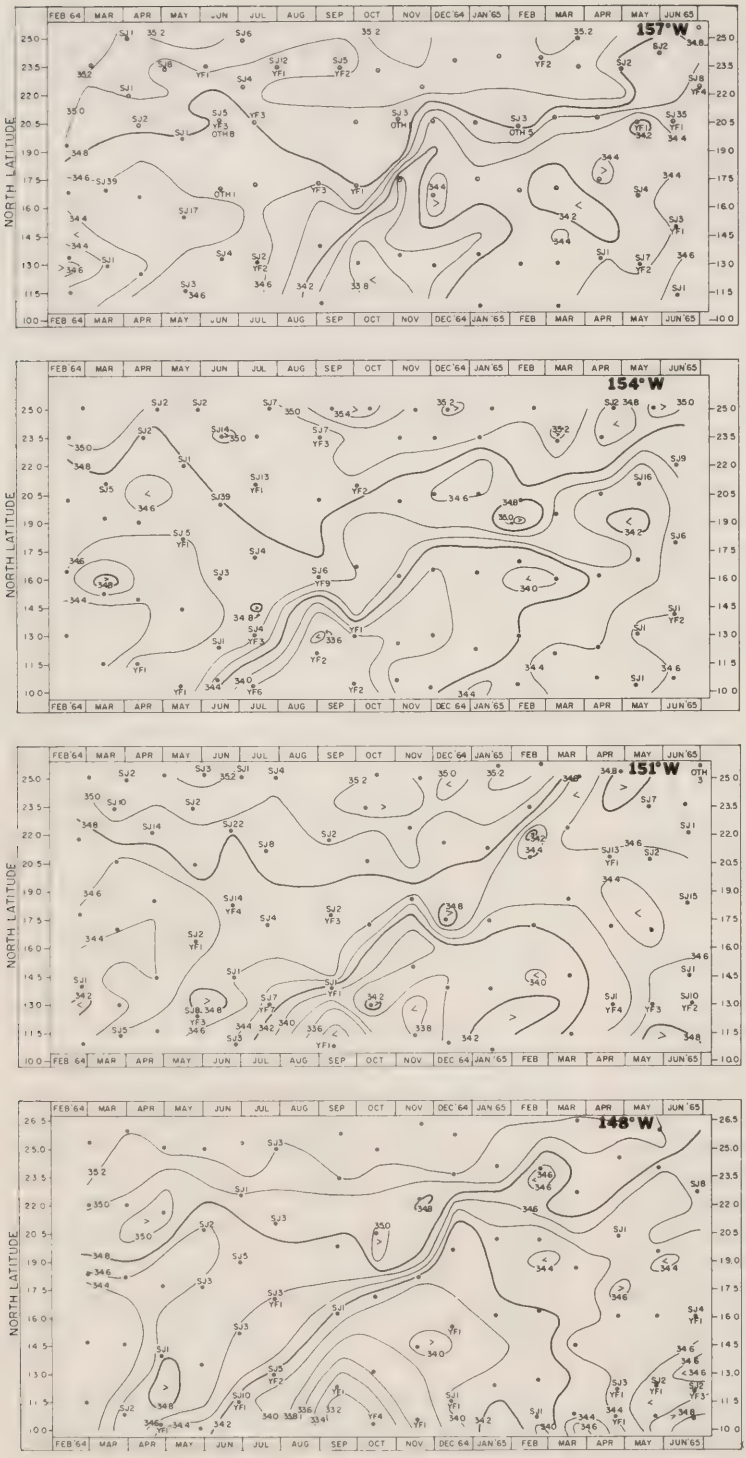

FIGURE 4.—Salinity (‰) distribution at 10 m, lat 10° to 26°N, long 148°, 151°, 154°, and 157°W, February 1964 to June 1965. Small circles indicate location of plankton tows. The number of skipjack (SJ), yellowfin (YF), and other tunalike larvae (OTH) captured are shown.

no fishery studies were undertaken to complement the oceanographic studies, results of the TWZO investigation augment the associations between skipjack and the environment that were described above. During each of the cruises, which lasted about 20 days, ½-hr plankton tows were made every evening between 8 and 9 o'clock with a 1-m net just below the sea surface. From each of the 19 or 20 plankton samples per cruise the tuna larvae were separated and identified.[4]

The descriptive results of the TWZO investigation have been summarized by Seckel (1968). Figure 4 shows the time variation in the meridional, 10-m salinity distribution for long 148°, 151°, 154°, and 157°W. The positions of the plankton tows and the number of skipjack, yellowfin or other tunalike larvae are superimposed on these graphs. The salinity isopleths 34.8‰ and 34.2‰ are drawn heavier to demark the southern boundary of the North Pacific Central water and the northern boundary of the North Pacific Equatorial water, respectively.

Along the meridian 157°W that passes through the Hawaiian Islands, the seasonal northward displacement in the spring of 1964 of the North Pacific Central water is evident. Subsequent southward retreat was stopped when a sharp northward displacement took place in October and November. Another sharp northward displacement of the 34.8‰ salinity isopleth took place in May. A pronounced feature along all meridians presented is the intrusion of the North Pacific Equatorial water during the spring and summer of 1964.

The TWZO observations spanned the entire 1964 and the beginning of the 1965 fishing seasons in Hawaii. With landings of 4,093 tons, 1964 fell into the normal category of fishing years (Figure 2b). Landings of 7,329 tons, in 1965, however, were the best on record and fall into the exceptional year category. The salinity distribution along long 157°W shows an important year-to-year difference in the meridional salinity gradient. During the winter and spring of 1964 the gradient was small or diffuse. During the winter and spring of 1965 the gradient was pronounced or high. Qualitatively, the differences in meridional gradients means that the currents were only weakly convergent in 1964 in contrast to the strong convergence or shear that existed in 1965.

This interpretation provides an additional lead towards an understanding of the association between the availability of skipjack and the environment. The concentration of organisms, whether drifting with the water, such as plankton, or swimming relative to the water, such as skipjack, is affected by water motion. Thus, the strongly convergent flow pattern evident from the high-salinity gradient would concentrate the skipjack schools and so increase their availability, unless, of course, the effect of the convergent flow is deliberately opposed. The concentrating effect is evident in Figure 5 showing the weekly skipjack landings in Hawaii and the Koko Head salinities. The sharp drop in Koko Head salinity at the beginning of May 1965 is coincident with the movement of the salinity gradient through the fishing area (Figure 4) and with the pronounced increase in weekly landings. A similarly pronounced change in landings with change in salinity was reported by Murphy et al. (1960).

Consider now the distribution of skipjack

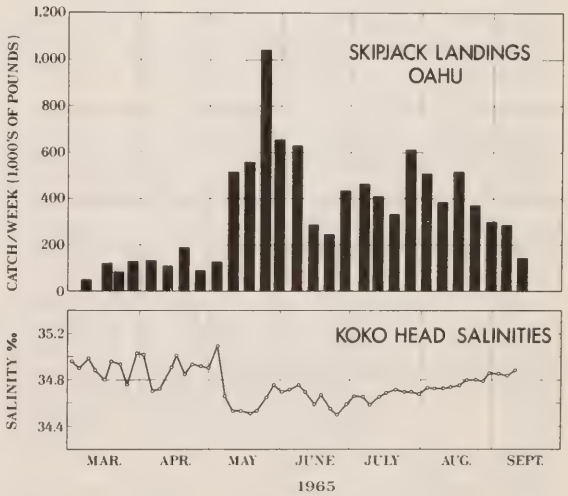

FIGURE 5.—Weekly skipjack landings at Oahu, March to September 1965 (upper panel), and Koko Head salinities (lower panel).

[4] The identifications of tuna larvae were made by Walter M. Matsumoto of the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory.

larvae shown in Figure 4. The size of skipjack larvae caught in plankton nets such as were used in the TWZO investigation range from 2.3 to 20.1 mm (Matsumoto, 1958). During the first month, growth is rapid and larvae may reach a length of 9 cm (Yoshida, 1971). Thus, presence of larvae indicates recent presence of adults. Only the presence or absence of larvae in a tow is considered, and tows with different larvae counts are not distinguished. General absence of larvae as between October 1964 and April 1965 may mean absence of adults or cessation of spawning. During the spring and summer of 1964 and spring of 1965, skipjack larvae, and therefore adults, occurred in all latitudes sampled during the TWZO cruises. The distribution, however, was not uniform. There were only few tows that captured larvae in water with a salinity above 35‰ and none in water with a salinity of less than 34‰.

Remembering that the salinity is used as an index of water type, the total number of plankton tows and the number of tows with skipjack larvae are listed in Table 2 as a function of salinity. The highest number of tows with skipjack larvae occurred in a salinity range from 34.61 to 34.8‰. Although there were 23 tows in water with a salinity below 34‰, no skipjack larvae were captured. The percentage of tows with larvae as a function of salinity is shown in Figure 6. The highest capture rate, 60%, occurred in water with a salinity of 34.61 to 34.8‰.

Quantitative sampling for tuna larvae is difficult and results must be interpreted with caution. However, during February to June of 1964 and 1965, 97 and 95 plankton tows were made, respectively. For all tows the same sampling procedures were followed. Interyear comparisons of the larvae capture rates, therefore, provide additional leads in gaining an understanding of the environment-skipjack relationship.

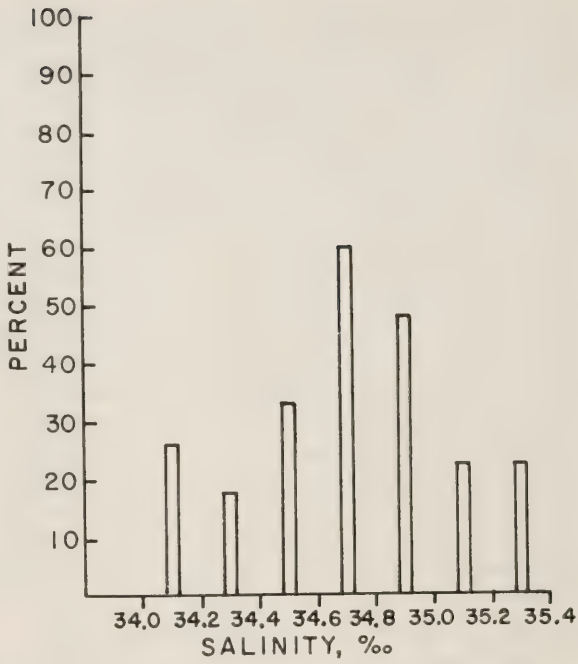

FIGURE 6.—Percent of plankton tows with skipjack larvae as a function of salinity from Trade Wind Zone Oceanography cruises, February 1964 to June 1965.

It is evident from Figure 4 that there were fewer tows with skipjack larvae in 1965 than there were in 1964. The number of tows with larvae and the total number of tows are listed in Table 3 for the cruises from February to June of each year as a function of salinity. With almost the same number of tows in each case, those with larvae in 1964 numbered 45 and those in

TABLE 2.—Summary of plankton tows with and without skipjack larvae as a function of salinity for all the Trade Wind Zone Oceanography cruises, February 1964 to June 1965.

Salinity Range ‰	33.01 –33.2	33.21 –33.4	33.41 –33.6	33.61 –33.8	33.81 –34.0	34.01 –34.2	34.21 –34.4	34.41 –34.6	34.61 –34.8	34.81 –35.0	35.01 –35.2	35.21 –35.4	35.41 –35.6	Total
Number of tows with skipjack larvae	0	0	0	0	0	6	7	18	34	21	9	5	0	100
Total number of tows	1	2	0	7	13	23	39	54	57	44	40	22	3	305

TABLE 3.—Summary of plankton tows with and without skipjack larvae as a function of salinity for the Trade Wind Zone Oceanography cruises, February to June 1964 and February to June 1965.

Salinity Range ‰		33.81 —34.0	34.01 —34.2	34.21 —34.4	34.41 —34.6	34.61 —34.8	34.81 —35.0	35.01 —35.2	35.21 —35.4	35.41 —35.6	Total
February to June 1964	Number of tows with skipjack larvae		2	2	3	16	12	5	5		45
	Total number of tows		2	11	16	26	17	13	12		97
February to June 1965	Number of tows with skipjack larvae		1	4	13	11	3				32
	Total number of tows	1	7	22	29	18	9	8	1		95

1965 numbered 32. This comparison is consistent with that made by Yoshida (1971) of the relative number of skipjack larvae found in billfish stomachs. The number of juveniles per 100 billfishes taken in 1964 was 21.3 and in 1965 the juveniles numbered 19.1.

The relative number of tows with larvae as a function of salinity for each year is shown in Figure 7. In 1964, although the total number of tows with larvae was highest in the 34.61 to 34.8‰ water, the highest capture rate was in 34.81 to 35.0‰ water. In 1965 highest capture rates were shifted to lower salinities. The highest percentage of tows with larvae, 60%, occurred in water with salinities of 34.61 to 34.8‰. The restrictions placed on the salinity index in the previous section is consistent with the capture rates of larvae during the TWZO cruises.

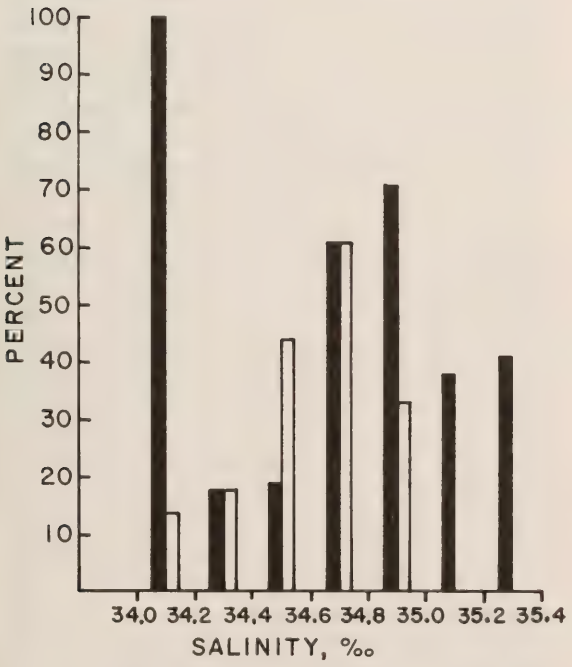

FIGURE 7.—Percent of plankton tows with skipjack larvae as a function of salinity from Trade Wind Zone Oceanography cruises, February to June 1964, solid bars, and February to June 1965, open bars.

It seems paradoxical that during 1965, the year with the highest skipjack landings in Hawaii, the number of tows with larvae (reflecting presence of adult skipjack) was lower than in 1964. Figure 7 shows that larvae were spread over a wider range of salinities in 1964 than in 1965, the difference occurring between 35 and 35.4‰. Although there were fewer tows in the high-salinity water during 1965 than during 1964, assuming the same capture rate as in 1964, there should have been three or four tows with larvae in the 35 to 35.4‰ salinity range during 1965. Thus, there were possibly as many or more skipjack in 1964 than in 1965 but their concentration was lower in 1964 resulting in lower Hawaiian landings. This picture is consistent with the salinity distribution, which had a high meridional gradient in 1965 as compared to 1964, reflecting stronger convergence.

Another possible cause for the difference in capture rates of larvae between 1964 and 1965 was recognized early in this century. Hjort (1914) suggested the possibility that the availability of food at the time of yolk absorption is

critical for the survival of larvae. In a large portion of the tropical and subtropical oceans food supply (plant production) may be governed by sea-air interaction processes. During the TWZO investigation there were large differences in sea-air interactions between the early parts of 1964 and 1965 (Seckel, 1970a,b). As an example, the heat of evaporation, $Q(E)$, the net heat exchange across the sea surface, $Q(N)$, and the zonal component of the wind stress, $\tau(x)$, for lat 17°N, long 152°W are listed in Table 4. The

TABLE 4.—Interyear differences of the heat of evaporation, $Q(E)$, the net heat exchange across the sea surface, $Q(N)$, and the zonal component of wind stress, τ_x, lat 17°N, long 152°W. $Q(E)$ and $Q(N)$ are positive if the sea gains heat, τ_x is positive to the east. (Seckel, 1970a,b.)

	$Q(E)$ cal cm^{-2} day^{-1}	$Q(N)$ cal cm^{-2} day^{-1}	τ_x dynes cm^{-2}
Jan-Apr 1964 average	−441	−44	−1.71
Jan-Apr 1965 average	−134	100	− .76
Interyear difference	307	144	.95

evaporation rate in January to April of 1964 was almost three times as large as during the same months of the following year. The sea-surface layer gained an average of 144 cal cm^{-2} day^{-1} more heat during the early part of 1965 than it did during the same time of 1964. The wind stress was more than twice as strong in 1964 than in 1965. Such interyear differences take place throughout the spawning areas of skipjack. For example, the large year-to-year temperature variations at Christmas Island (Seckel and Yong, 1971) reflect large changes in sea-air interaction processes.

IMPLICATIONS OF ENVIRONMENTAL ASSOCIATIONS

THE DRIFT HYPOTHESIS

The pronounced salinity gradient at the boundary of the North Pacific Central water in 1965 (Figure 4) implies strong convergence. Organisms drifting or skipjack schools swimming in the converging currents also converge into the boundary region. The availability of fish is therefore expected to be larger within than outside of the zone of convergence. Interyear differences in the intensity of convergence as reflected by the meridional salinity gradient in the springs of 1964 and 1965 contribute to the interyear differences in availability. The boundary or convergence zone need not remain at the same location and may shift northward as indicated by the low Koko Head salinities during 1968 and 1969. Consequently, fish concentrations were also shifted out of the Hawaiian fishing grounds resulting in the low landings for these years.

The convergence of skipjack schools concept can be applied on a broader scale. Rothschild (1965) postulates that a component of Hawaiian-caught skipjack originates in the eastern Pacific. This hypothesis is supported by the recapture of fish in Hawaiian waters that were tagged in the eastern Pacific (Table 5).[5] Consider now skipjack schools that entered the North Equatorial Current in the eastern Pacific. Throughout the time while the skipjack schools are carried westward by the current, they are also displaced northward by a meridional component of the trade wind-driven surface current. The magnitude of the mean annual westward component of wind stress long 120° to 160°W between lat 10° and 25°N (University of California, 1948) is shown schematically with the associated northward component of the wind-driven surface current in Figure 8. Under these wind conditions an object would take on average about 22 months to drift from lat 10° to 20°N.

Figure 8 also shows that the northward wind-driven current decreases with increasing latitude. The number of skipjack schools drifting from the 10°-15° into the 15°-20° latitude band is larger than the number drifting from the 15°-20° to the 20°-25° latitude band. In other words, schools in the North Equatorial Current would converge north of lat 15°N.

These qualitative considerations can be expressed numerically. The displacement of a fish school, S, during a time interval, Δt, is

[5] Tagging data were kindly supplied by Dr. William H. Bayliff, Inter-American Tropical Tuna Commission.

$$\Delta S = V\Delta t.$$

The velocity of the fish school, V, consists of two parts: the velocity of the water relative to fixed coordinates, V_W, and the velocity of the school relative to the water, V_F. The displacement equation is

$$\Delta S = (V_W + V_F)\ \Delta t.$$

The velocities are functions of location and of time and the net displacement of a school after a time T is

$$S = \sum_{i=1}^{n} [(V_W + V_F)\Delta t]_i$$

or

$$S = S_W + S_F = \sum_{i=1}^{n} (V_W\Delta t)_i + \sum_{i=1}^{n} (V_F\Delta t)_i$$

with $T = n\Delta t$ if the time increments are all equal.

Although this displacement equation is true for any time and space scale, current or swimming velocities averaged over time intervals, Δt, of a week or a month are of interest here. Random motions of fish schools and eddying currents therefore make no contribution to the net displacement in the scales under consideration. It is evident that in migrations of thousands of kilometers taking a time of 1 to 2 years, ocean currents cannot be ignored unless

$$V_W << V_F$$

and the displacement of the school due to the current, S_w, is therefore small compared to that relative to the water.

If the environmental conditions are known, then a numerical integration can be performed to determine the displacement of a fish school caused by currents alone. An example of a drift model that is applicable to skipjack originating in the eastern North Pacific will be given in a subsequent section.

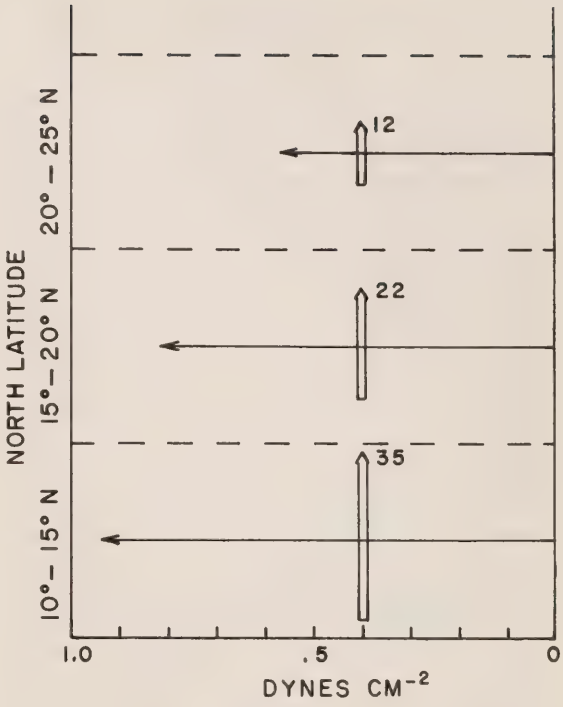

FIGURE 8.—Schematic presentation of average zonal wind stress, long 120° to 160°W, in latitude bands 10°-15°N, 15°-20°N, 20°-25°N, and associated meridional component of wind-driven current in miles per month (thick arrows).

TABLE 5.—Skipjack tagged in the eastern Pacific and recaptured in the central Pacific.

Tag release		Tag recapture		
Date	Area	Date	Area	Days free
17 Apr. 1960	Revillagigedo Is.	22 Aug. 1962	Hawaii	858
5 Sept. 1960	Baja California	12 June 1962	Hawaii	646
22 Sept. 1961	Baja California	5 Apr. 1963	Christmas Is.	561
5 June 1965	Revillagigedo Is.	27 June 1967	Hawaii	753
6 Nov. 1969	Clipperton Is.	21 July 1970	Hawaii	258
6 Nov. 1969	Clipperton Is.	8 Aug. 1970	Hawaii	276
26 Oct. 1969	lat 4°11′N, long 119°02′W	14 July 1971	Hawaii	627

Data source: Dr. William H. Bayliff, Inter-American Tropical Tuna Commission.

LARVAL SURVIVAL AND YEAR-CLASS STRENGTH

Rothschild (1965) conceded that environmental conditions a few months prior to the Hawaiian fishing season affect the availability of skipjack but felt that the large variability in catch rates is due to variability in the year-class strength. The variability in catch rates is also apparent within the two broad categories of years defined earlier in this paper. In the next section it will be shown, however, that the variability can be caused by variations in the current field. Nevertheless, year-class strength is not excluded as an additional cause for the variations in catch rates. It was previously noted that the large interyear differences in sea-air interaction processes observed during the TWZO investigation would affect productivity (plant production) and, hence, also larval survival. In mid- and high latitudes, winter overturn regularly replenishes the nutrients of the surface layer. In a large portion of the tropical and subtropical ocean this cyclical replenishment does not take place and a permanent pycnocline inhibits vertical exchange of the surface nutrient-deficient with the deeper nutrient-rich water. Other than in areas of upwelling such as along the equator and possibly near islands, nutrients enter the surface layer by eddy diffusion. A net heat gain in the tropical and subtropical oceans tends to increase the stability of the pycnocline and thus inhibits the eddy diffusion process. Wind stirring, vertical current shear, and internal waves tend to enhance eddy diffusion. The wind speed also affects the evaporation which, in turn, affects the net heat exchange across the sea surface. The evaporation rate may be so large that there is a net heat loss from the sea surface and convective overturn takes place, increasing the nutrient supply of the surface layer.

Increased vertical diffusion across the pycnocline due to favorable sea-air interactions may have subtle effects in that it need not be reflected as an increase in nutrient concentration. In areas where nutrients limit productivity, an increase in the nutrient supply into the surface layer can be entirely exhausted by an increase in productivity. Thus, a low phosphate concentration and absence of a seasonal variation in the trade wind region of the North Pacific Ocean does not preclude variations in productivity.

The sea-air interactions in the trade wind zone from January to April 1964 (Table 4) favor a larger nutrient supply by diffusion and, therefore, higher productivity than do those for the same months of 1965. Consequently, a better supply of primary producers in 1964 should have enhanced larval survival. The TWZO larval captures in 1964 and 1965 are consistent with this proposition. There is presently no information to verify the hypothetical sequence of events.

In this discussion the results of the TWZO investigation are used to illustrate what probably takes place throughout the tropical and subtropical oceans and, therefore, in all the skipjack spawning areas. The illustration does not imply that the North Equatorial Current or the Hawaiian waters are major skipjack spawning grounds.

The sequence of events described is amenable to quantitative study. Productivity models exist, such as the one used by Parsons and Anderson (1970), that can be adapted to reflect the environmental changes of the skipjack spawning areas. An integral part of the productivity studies must be adequate sampling of the animal community, including skipjack larvae, that directly depend on the initial stages of the food chain. Those studies would lead to a recruitment or year-class strength model that complements the drift model. Development of a year-class strength model is not within the scope of this paper.

A DRIFT MODEL

The displacement of a fish school was expressed above by

$$S = S_W + S_F.$$

Here I wish to consider only the contribution to the total displacement of fish schools caused by the currents, S_W, in a portion of ocean between lat 10° and 25°N, and long 120° and 160°W, the model ocean. In this idealized, rectangular ocean the distances between degrees of latitude and

longitude are equal, and there is a geostrophic current and a wind-driven current. The increments of displacement of a fish school or a drifting object by currents are expressed by

$$\Delta S_W = V_W \Delta t = (V_G + V_E)\Delta t,$$

where V_W, the velocity of the water, is the sum of the geostrophic current, V_G, and the wind-driven current, V_E. V_G and V_E are functions of position and of time. Because the velocities are vectors, numerical integration (summation of increments) is facilitated by using zonal and meridional components of the displacement

$$\Delta X = (V_{GX} + V_{EX})\ \Delta t,$$

$$\Delta Y = (V_{GY} + V_{EY})\ \Delta t, \text{ respectively.}$$

The position of the fish school after n equal increments of time, Δt, is

$$X_n = X_0 + (V_{GX} + V_{EX})_1 \Delta t + (V_{GX} + V_{EX})_2 \Delta t + \ldots + (V_{GX} + V_{EX})_n \Delta t,$$

$$Y_n = Y_0 + (V_{GY} + V_{EY})_1 \Delta t + (V_{GY} + V_{EY})_2 \Delta t + \ldots + (V_{GY} + V_{EY})_n \Delta t$$

with an initial position X_0, Y_0.

In the model rectangle of ocean the meridional distribution of dynamic height varies sinusoidally according to

$$A_0 + C(t) \cos \frac{2\pi}{L(x)}(y - \alpha).$$

The minimum dynamic height is at lat 10°N and the maximum slopes northward from lat 20°30′N at long 160°W to lat 26°30′N at long 120°W (Figure 9). Thus, the geostrophic flow is zonal near lat 10°N but acquires a meridional component at higher latitudes. The amplitude of dynamic height, $C(t)$, in the sinusoidal distribution varies seasonally. The zonal component of the geostrophic current is expressed analytically by

$$V_{GX} = -K_i \left(\frac{2\pi}{L(x)}\ C(t)\ \sin \frac{2\pi}{L(x)}\ (y - \alpha) \right).$$

The seasonal variation of the amplitude,

$$C(t) = -[0.142 + 0.05 \cos 30(t + 1.13)],$$

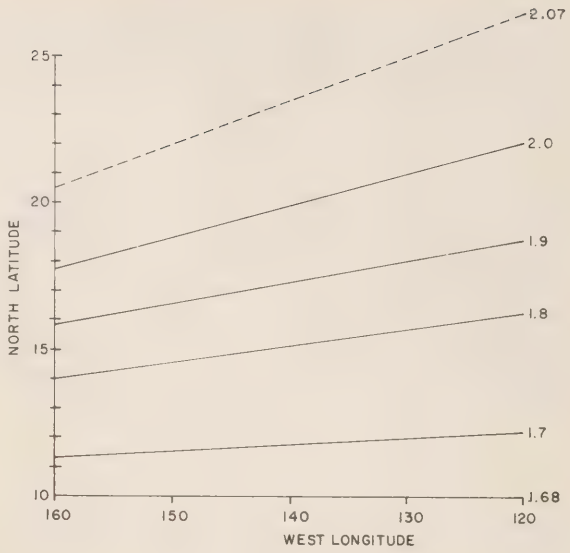

FIGURE 9.—Dynamic topography of model ocean (dynamic meters) at the time of maximum velocity.

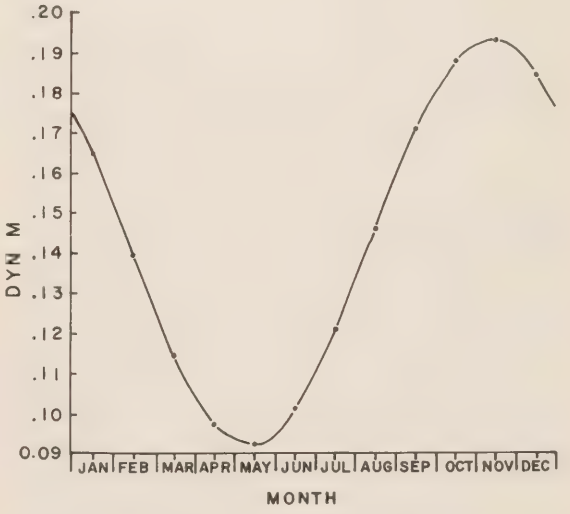

FIGURE 10.—Seasonal variation in amplitude, $C(t)$, for the harmonic expression of dynamic height as a function of latitude.

is shown in Figure 10.

The wave length, a function of longitude, x, is twice the width of the current: $L(x) = 69 - 0.3x$.

The meridional component of geostrophic current is given as a function of latitude, y, longitude, x, and the zonal component of geostrophic current, V_{GX}:

$$V_{GY} = -\frac{(y-10)}{230-x} V_{GX},$$

where x and y are the degrees of longitude and latitude in the model ocean, with the coordinates positive westward and northward. $L(x)$ is given in degrees latitude, and t is the time of the year in months. The phase angle, α, equals 10°, and in the dynamic height expression A_0 equals 1.875 dyn m. The zonal component of geostrophic flow in cm sec^{-1} is given by

$$K_1 = \frac{61.69}{\sin y}.$$

In the drift model it is most convenient to express the flow in nautical miles per month with

$$K_1 = \frac{862.9}{\sin y}.$$

The wind-driven current is based on the wind stress values of the Scripps Institution of Oceanography (University of California, 1948). The zonal and meridional components of stress were averaged between long 120° and 160°W for each month of the year and each latitude band 10°-14°N, 15°-19°N, and 20°-24°N. The variation with time, t, of the zonal components, τ_x, and the meridional components, τ_y, of the wind stress are adequately defined by the harmonic functions in Table 6, and shown in Figure 11.

The meridional and zonal components of Ekman transport are calculated from the equations $E_y = -\tau_x/f$, and $E_x = \tau_y/f$, where f is the Coriolis parameter. Most of the transport takes place in the upper 100 m of ocean. Here, it is assumed that all the transport takes place in the upper 100 m. $V_{EX} = -K_2 \tau_y$ and $V_{EY} = K_2\tau_x$ then give the mean wind-driven current for this depth in cm sec^{-1} if K_2 for latitude bands 10°-14°N, 15°-19°N, and 20°-24°N is 3.17, 2.29, and 1.79, respectively. Again, for application in the drift model it is most convenient to express the drift current in nautical miles per month, and K_2 for latitude bands 10°-14°N, 15°-19°N, and 20°-24°N becomes 37.5, 27.0, and 21.3.

TABLE 6.—Harmonic functions of the zonal component, τ_x, and meridional component, τ_y, of wind stress in dynes cm^{-2}. The time of year, t, is in months.

lat 10°-14°N,	$\tau_x = 0.91 + 0.544 \cos 30\ (t-2.1)$
lat 15°-19°N,	$\tau_x = 0.8 + 0.188 \cos 30\ (t-1.2)$
lat 20°-24°N,	$\tau_x = 0.56 + 0.022 \cos 30\ (t+1.2)$
lat 10°-14°N,	$\tau_y = 0.56 - 0.330 \cos 30\ (t-2.5)$
lat 15°-19°N,	$\tau_y = 0.47 - 0.04 \cos 30\ (t-0.2)$
lat 20°-24°N,	$\tau_y = 0.34 + 0.045 \cos 30\ (t-1.4)$

Using the geostrophic and wind-driven current speeds, the drift displacements can be calculated. Once per month 11 objects are introduced along the eastern boundary of the model ocean, equally spaced from lat 10° to 20°N. Displacements are calculated and the new position at the end of the month is determined. Again, displacements are calculated for the new time and position, and the positions at the end of the second month determined. These calculations are repeated for 36 months or stopped before that time if the western boundary (long 160°W) is crossed or when the object drifts into easterly (negative) flow at the northern boundary of the westerly setting geostrophic current. It is assumed that the drifting objects move up and down in the upper 100 m much as a skipjack school may be doing.

The result of the numerical integration is shown in Figure 12. The location of drifting objects that were introduced at the beginning of April, May, and June at lat 10° to 20°N along long 120°W are traced across the model ocean in steps of 3 months. After 12 months all drifting objects are north of lat 15°N. The objects that began north of lat 15°N are the first to drift into the northern, slow portion of the Equatorial Current and are overtaken by the objects that began at and to the south of lat 15°N. Thus a meridional distribution of objects at the beginning becomes oriented along the northern edge of the model equatorial current after 24 months of drifting.

Another presentation of the results (Figure 13) shows the location, after 30 months, of all objects that were introduced at the beginning of each of the 30 months along long 120°W. The most westerly position reached by objects during each quarter is indicated by a dotted line. Again, it is evident that objects initially located south

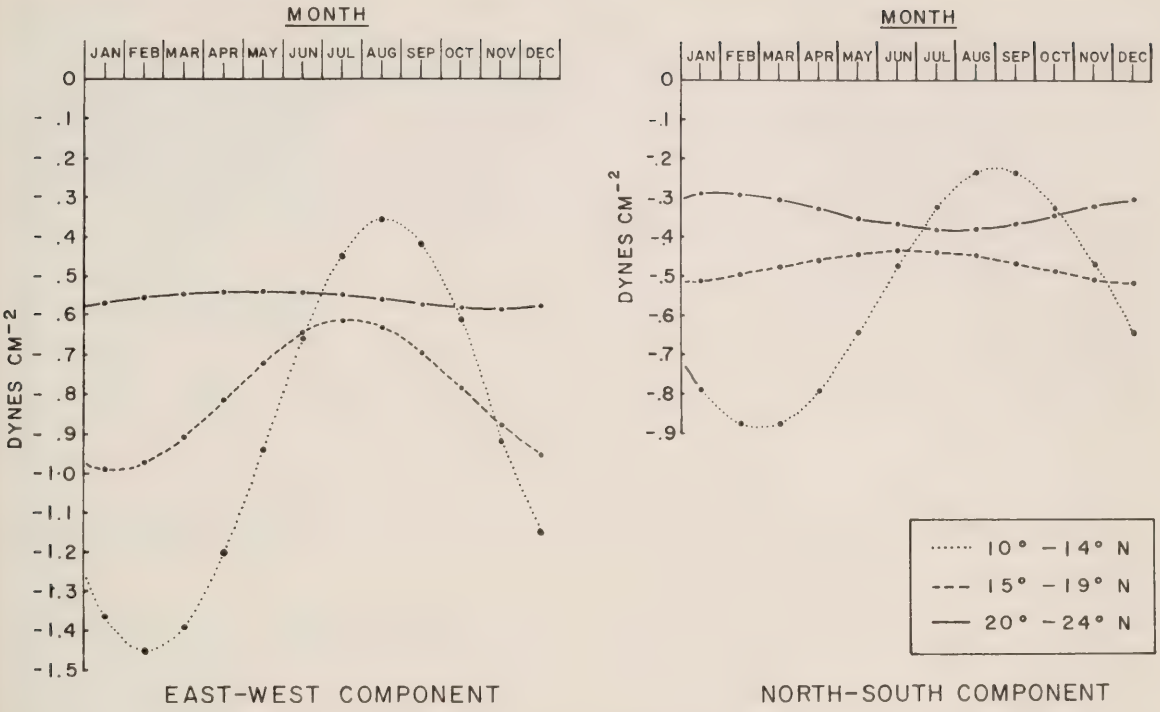

FIGURE 11.—Zonal and meridional components of wind stress in latitude bands 10°-14°N, 15°-19°N, 20°-24°N averaged between long 120° and 160°W (University of California, 1948). Stress is positive if directed to the east and north, respectively.

of lat 15°N rapidly drift northward. Objects appear to concentrate on the southern and northern edge of their distribution and then merge west of long 150°W in a relatively narrow band between lat 18° and 22°N. Lost in the presentation are a few objects that drifted across the northern edge of the equatorial current in the western portion of the model ocean and those that drifted west beyond long 160°W. In the western part of the model area considerable mingling of objects introduced in different seasons takes place. In some 1-degree units of area are found objects that were introduced during 3 seasons.

The concentration of drifting objects at the southern edge of their distribution is caused by the seasonal difference in the convergence of the meridional wind-driven current. The zonal component of the trades is stronger from November to June at lat 10° to 14°N then at lat 15° to 19°N but weaker from June to November (Figure 11). Consequently, the meridional component of wind-driven current is strongly convergent from November to June but weakly convergent or divergent during the remainder of the year. The effect of this seasonal difference is illustrated in Figure 14. Note that in the first case with a high meridional wind-driven current only 4 objects are left south of lat 15°N but 11 objects are left in the second case. Again, in the first case with strong meridional convergence there were 14 objects between lat 15° and 17° but 8 objects for the second case.

The seasonal variation of meridional wind-driven current inferred from the lat 15° to 19° and 20° to 24°N curves in Figure 11 is smaller than it is south of lat 15°N. Consequently the northward drift near lat 20°N is not as large as in the example given above. Near this latitude, however, the southward component of the

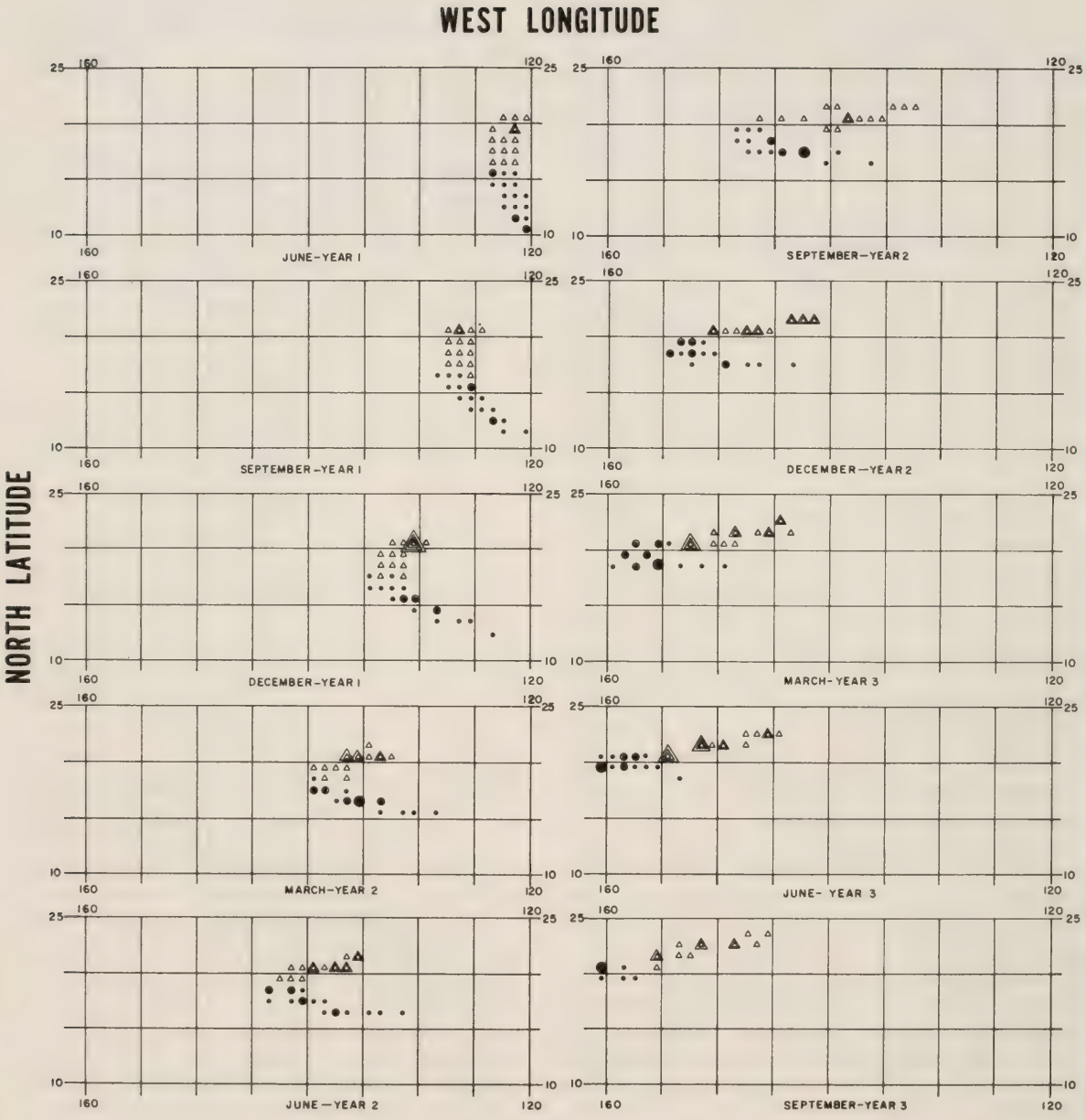

FIGURE 12.—Location of drifting objects every 3 months after being introduced during April, May, and June of the first model year at long 120°W. Triangles denote objects introduced north of lat 15°N. The number of drifting objects, if there are more than one per 1-degree square, is indicated by concentric triangles or circles.

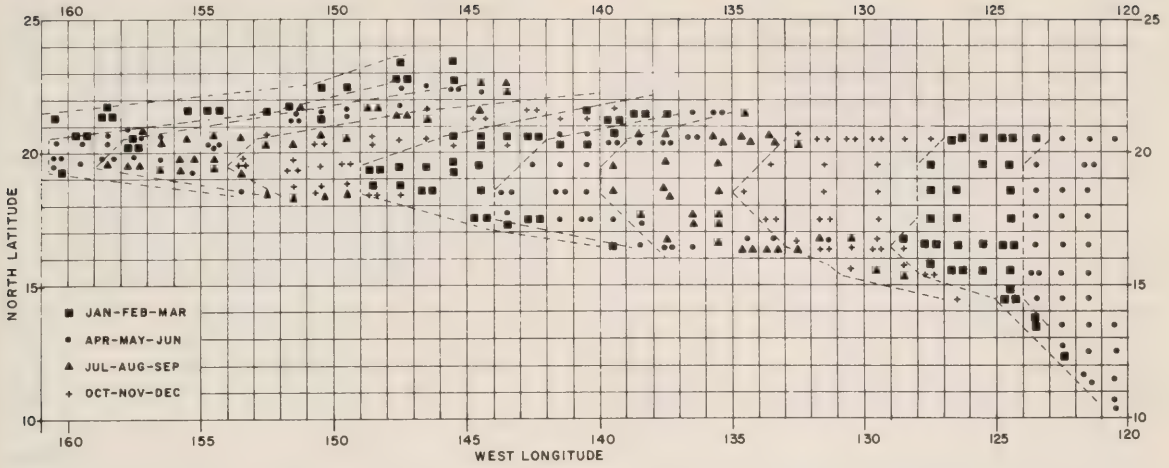

FIGURE 13.—Locations of drifting objects in June of the third model year that were introduced in each of the previous 30 months at long 120°W. Dashed lines indicate most westerly location reached by objects introduced every quarter.

geostrophic current (Figure 9) becomes important. The effect of convergence of this component of flow with the northward wind-driven current is evident at the northern edge of the distribution of drifting objects in Figure 13.

As the objects drift westward north of lat 18°N and west of long 140°N, they enter the region of decreasing speed in the North Equatorial Current (Figure 9) and therefore tend to accumulate further (Figure 13).

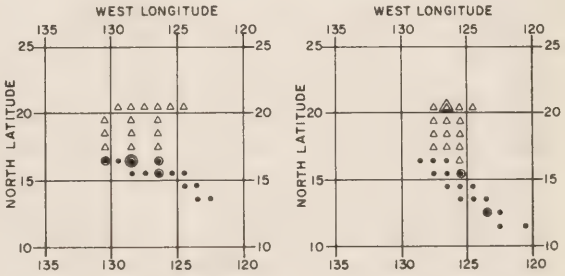

FIGURE 14.—Left Panel: Position of objects in March that were introduced at long 120°W during the previous October, November, and December. Right panel: Positions of objects in September that were introduced at long 120°W during the previous April, May, and June.

THE MODEL OCEAN AND SKIPJACK

The minimum duration of drift of objects from long 120°W to the quadrant north of lat 19°N and west of long 155°W ranges from 21 to 23 months (Table 7). These times are of the same order of magnitude as the times skipjack tagged in the eastern Pacific were free except for the two skipjack tagged near Clipperton Island (Table 5). If the model ocean is realistic, these results indicate that the mean velocity of the fish relative to the water (V_F) is small compared to the mean velocity of the water (V_W). The paths of the fish, of course, are not known and many routes and modes of travel behavior can be postulated. However, there is one, the simplest mode

TABLE 7.—Minimum duration of drift from long 120°W to the quadrant north of lat 19°N and west of long 155°W.

Month of start	Year and month of arrival		Duration of drift in months
Jan.	2d	Oct	22
Feb.	2d	Nov	22
Mar.	2d	Dec	22
Apr.	3d	Jan	22
May	3d	Jan	21
June	3d	Feb	21
July	3d	Mar	21
Aug.	3d	Apr	21
Sept.	3d	Jun	22
Oct.	3d	Aug	23
Nov.	3d	Sep	23
Dec.	3d	Oct	23

of travel, that must be considered—namely, randomly swimming skipjack drift westward in the North Equatorial Current. This mode of travel means that skipjack entering the North Equatorial Current in the eastern Pacific do not migrate in the sense that they are actively swimming towards a destination. These skipjack are concentrated, or converge with the trade wind-driven water near lat 15°N, and near lat 20°N they are concentrated by the southward component of the geostrophic current and the northward component of wind-driven current. As the fish schools approach Hawaii, they further accumulate because of decreasing geostrophic flow.

COMPARISON OF THE MODEL WITH THE REAL OCEAN

In the model the effects of characteristic features in the geostrophic and wind-driven currents on the distribution of drifting objects were demonstrated. The simplest analytic expressions for the North Equatorial Current and the wind distribution were used in order to facilitate numerical integration. How well do these simple expressions reflect the average conditions as we know them to exist in the ocean?

First, consider the field of geostrophic flow. In the model area, data from historic oceanographic cruises are sparse, but a chart of the Pacific Ocean dynamic topography prepared by Reid (1962) shows that maximum and minimum dynamic heights differ by about 0.4 dyn m as they do in Figure 9. Average geostrophic speeds in the model and the ocean are therefore of the same magnitude.

There is some uncertainty in the width of the North Equatorial Current at long 120°W. At this meridian Reid's chart shows the northern edge to be at about lat 15°N. A qualitative geostrophic interpretation of Barkley's (1968) depth of the sigma-t 25.4 surface, in the main pycnocline, places the northern edge near lat 25°N at long 120°W and near lat 21°N at long 160°W.

Many more bathythermograph data than oceanographic station data are available. A geostrophic interpretation of Wyrtki's (1964) depths of the center of the permanent thermocline places the northern edge of the Equatorial Current to the north of lat 20°N in the eastern part of the model area. More recently, charts of the temperature distribution at 400 ft prepared from bathythermograph data by Robinson and Bauer[6] places the northern edge of the Equatorial Current near lat 18° or 19°N at long 160°W and from about lat 20° to 25°N at long 120°W. In the vicinity of the Hawaiian Islands, the northern edge of the Equatorial Current inferred from Robinson's charts compares well with the results of the TWZO investigation (Charnell, Au, and Seckel, 1967a,b,c,d,e,f).

The seasonal variation of the geostrophic flow in the North Equatorial Current observed during the TWZO investigation was reported by Seckel (1970c). The meridional slope of dynamic height between lat 10° and 20°N computed for each cruise of this investigation, reflecting the mean, zonal component of geostrophic current

[6] Robinson, M. K., and R. A. Bauer, Atlas of monthly mean sea surface and subsurface temperature and depth of the top of the thermocline, North Pacific Ocean. Unpublished manuscript reproduced by Fleet Numerical Weather Central, 1971.

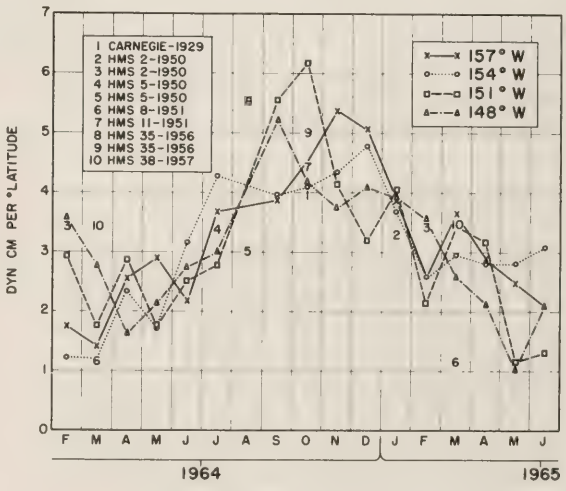

FIGURE 15.—Meridional slopes of dynamic height, lat 10° to 20°N for every month from February 1964 to June 1965 of the Trade Wind Zone Oceanography cruises, connected by straight lines. Numerals indicate the meridional slopes of dynamic height for the cruises of the *Carnegie*, 1929, and *Hugh M. Smith* (HMS), 1950-1957.

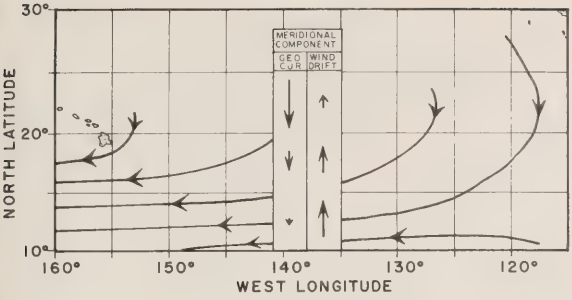

FIGURE 16.—Schematic presentation of geostrophic flow in the North Equatorial Current with meridional components of geostrophic flow and wind-driven current (insert).

is shown in Figure 15. Also shown are the meridional slopes computed from historic cruises. These values fall into the seasonal pattern. Qualitative interpretations of Wyrtki's and Robinson's charts referred to above confirm the TWZO results and show that the seasonal variation extends to long 120°W.

The model east-west component of geostrophic flow, therefore, compares well with available oceanographic station and bathythermograph data. Although a small north-south component of geostrophic flow is computed from the analytical expression of dynamic height used in the model, this component is not adequately represented. A schematic presentation of geostrophic flow in Figure 16 illustrates that south of lat 15°N the Equatorial Current is essentially zonal but north of this latitude, the meridional component increases to north of lat 20°N where the geostrophic current is mostly meridional.

The underestimate of the meridional component of geostrophic flow in the northern portion of the model has the effect of shifting the main concentration of drifting objects north. The underestimate, however, does not affect the duration of east to west drift.

In the model only drift within the North Equatorial Current is considered and objects that pass across its northern boundary are not plotted in Figures 12 and 13. In the ocean, drifting objects that pass across the northern boundary are carried back into the convergence by easterly and southerly components of geostrophic flow. Thus, the concentration of drifting objects in the convergence near Hawaii is expected to be larger than shown in the model.

The wind stress values of the Scripps Institution of Oceanography (University of California, 1948) that were used represent average conditions in the trade wind region. Important in the drift model is a northward component of wind drift that is proportional to the zonal component of wind stress. This characteristic feature is not lost by averaging wind stress values in 5-degree latitude bands between long 120° and 160°W.

The simple procedure of dividing the Ekman transport by 100 m to obtain the wind-driven current may be questioned. This procedure, however, affects the magnitude of wind drift and not the characteristic feature essential in the drift model; a meridional component of wind-driven current.

The results of the drift model are therefore the same as those to be expected in the portion of ocean under consideration if average conditions prevail. Drifting objects or skipjack schools uniformly distributed along long 120°W between lat 10° and 20°N drift westward and southward with the geostrophic North Equatorial Current. A component of surface wind-driven current in the direction to the right of the wind stress vector displaces the skipjack schools northward. In consequence of the converging flow fields, the concentration of drifting schools increases westward much as in the model.

The drift model is based on a smooth North Equatorial Current representing average conditions. From Figure 17, showing the time variation of the east-west component of geostrophic flow at long 148°W during the TWZO investigation, it is evident that the North Equatorial Current is not a smooth flowing stream. Cells of high westerly speeds alternate with low speeds or even easterly flow directions. A fish school caught in high westerly flow of more than 25 cm sec^{-1}, such as occurred near lat 15°N during August to October 1964, would in 2 months be carried about 1,300 km (700 nautical miles) westward. Thus, much shorter drift durations can occur than those given in the model. An

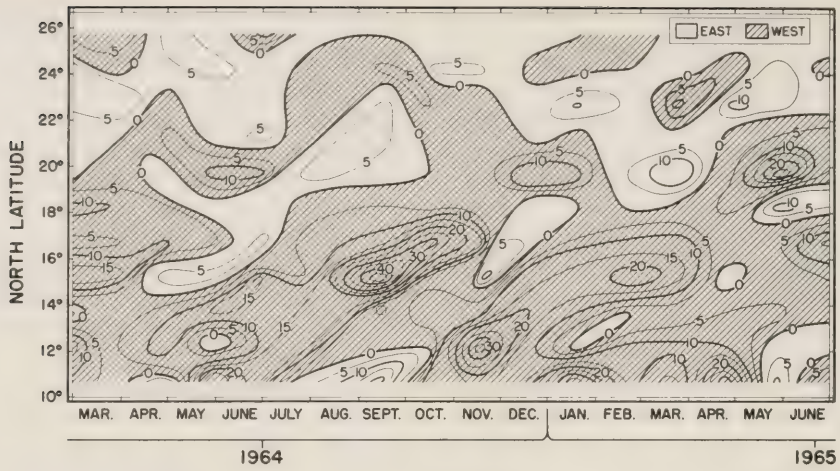

FIGURE 17.—Zonal component of geostrophic flow (cm sec^{-1}) at long 148°W from Trade Wind Oceanography cruises, March 1964 to June 1965. Hatching indicates flow to the west.

example are the skipjack that were tagged near Clipperton Island (Table 5).

Large interyear differences in mean geostrophic flow take place. Between March of 1964 and 1965, the average geostrophic speeds, as interpreted from the meridional slopes of dynamic height, Figure 15, differed by more than a factor of two. In August, historic cruise data indicate a factor of 1.8 in the interyear difference. Large interyear differences in wind stresses as listed in Table 4 also occur (Seckel, 1970b). The path of a drifting skipjack school therefore is expected to vary from year to year. Also to be expected are year-to-year changes in location and intensity of the converging southward component of geostrophic flow with the northward component of wind drift, as evidenced in Figure 4.

SUMMARY AND DISCUSSION

Oceanographic studies have led to the discovery of environmental changes that are associated with the seasonal and interyear differences in availability of skipjack to the Hawaiian fishery. Important is the seasonal northward movement in spring and summer of low salinity, California Current Extension water that replaces high salinity, North Pacific Central water in the Hawaiian region. Intrusion of the California Current Extension water coincides with the seasonal increase of skipjack landings. Koko Head salinities as well as the larval distributions observed during the TWZO investigation indicate that the high salinity range (34.6 to 34.8‰) of the California Current Extension is most favorable. Failure of this water to move into the fishing region results in low catches.

Northward movement of surface water during late winter and early spring causes warm advection or a warming of the water earlier than can be expected from heat exchange across the sea surface. If initial warming occurs before the end of February catches tend to be good. Initial warming in March indicates unfavorable conditions.

Using as indices the time of initial warming and the spring and summer salinity in the Hawaiian Islands, one finds that catches are normal when either or both indices are unfavorable, and exceptional when both indices are favorable. Normal annual catches average 3,600 tons and range from 2,700 to 4,400 tons. Exceptional annual catches average 5,800 tons and range from 4,940 to 7,330 tons.

Both indices reflect dynamic conditions in the environment. This view is supported by results of the TWZO investigation. A diffuse salinity

gradient separating the North Pacific Central water from the California Current Extension water in 1964 (Figure 4) coincided with a normal fishing year, a sharp gradient in 1965 coincided with an exceptional year. The character of the gradient is determined by the currents.

The importance of currents in marine biology is recognized. Examples of how currents affect marine life have been given by Laevastu and Hela (1970). However, the active part that ocean currents play in the migration of adult fish has not been stressed. The role of currents in fish migrations including the movements of fish without reference to landmarks has been described by Harden Jones (1968). The role has been covered only qualitatively, however, and tuna migrations were not amongst his examples.

The destination and migration path of a fish is the vector sum of the water velocity and the swimming velocity relative to the water. The contribution of the currents to the migration of skipjack that enter the North Equatorial Current in the eastern Pacific has been examined by means of a simple drift model. Essential in this model are the geostrophic flow of the North Equatorial Current and a northward component of surface wind-driven current resulting from the trades. In this current system floating objects or fish schools uniformly distributed between lat 10° and 20°N at long 120°W would be concentrated by the meridional component of wind-driven flow as they drift westward.

This concentrating mechanism is evident in Figure 13 where the southern boundary of the drifting objects (fish schools) shifts northward with increasing west longitude. Additionally, objects (fish schools) are concentrated where a southerly component of geostrophic flow and a northerly component of wind drift converge north of lat 20°N (Figure 13). The minimum time required to reach the Hawaiian Islands ranges from 21 to 23 months (Table 7). The computed drift time is of the same magnitude as the time of freedom of tagged fish (Table 5).

Before examining the consequences of this result, it is useful to place some limits on the navigational abilities of skipjack. (See also Harden Jones, 1968.) In terms of physics, it is hard to understand how, in the open ocean without a fixed reference, a fish knows that he is in a current. Only in accelerating flow would he be able to feel a force. The fish, therefore, does not know whether he is swimming with or against the current.

Easier to understand is the ability of a fish to swim in the direction of his choice. He may also know from the water properties, the type of forage, or from celestial navigation, that he is not in the area of his choice and therefore may set a course for a more desirable environment. Even in this eventuality, his destination is affected by the current.

Thus, the distribution of skipjack, whether they swim randomly and drift with the current or swim in a predetermined direction, is affected by the northward component of the wind-driven current and the convergence near the northern edge of the Equatorial Current.

As a result of the numerical model it can be postulated that a possible, and the simplest, mode by which skipjack travel from the eastern Pacific to Hawaii, is by swimming randomly and drifting with the current. This mode of travel is consistent with the empirical associations that were described and does not contradict the applicable portion of Rothschild's (1965) migration model. Rothschild statistically related the time of warming in Hawaiian waters with annual landings and stated " . . . that 44 percent of the variation in catch is accounted for by time of warming, the other 56 percent being unexplained." This statement can be misinterpreted in that it implies a causal relation between time of warming and catch rates. Rothschild apparently wishes to demonstrate that there is a variation in catch rates that is not associated with the variation of time of warming. This conclusion is also evident from Figure 2 which shows a relatively large range of catch rates within the exceptional and normal types of years. Rothschild examined the differences and their causes in the size frequency distributions of the eastern North Pacific and Hawaiian skipjack fisheries. He concluded " . . . that year-class associated phenomena play an important role in controlling the abundance of skipjack in Hawaiian waters." Rothschild, however, neglected to consider the effects of currents on the distribution of skipjack.

Currents, as is evident from the drift model results, also cause variability in annual landings and in the size-frequency distributions. It was noted that in the western portion of the model, drifting objects were found in a single degree-square area that had been introduced along long 120°W during 3 seasons. If the drifting objects are fish schools an age difference of 9 months would be reflected in the sizes of fish caught.

TWZO results have shown that the mean geostrophic flow in the North Equatorial Current can vary by up to a factor of 2 from year to year and that there are large interyear differences in the wind stress. The time of drift from the eastern to the central North Pacific can therefore vary more than the range indicated by the drift model, and it is possible for skipjack schools that entered the North Equatorial Current during 1 year to catch up with those that entered during the previous year.

Rothschild (1965) also states that lack of growth, or slow growth, as reflected by size frequency distributions, can be due to a movement of fish through the fishery. This movement can be fish schools drifting with the currents.

The size of fish caught in the Hawaiian fishery is also affected by the time, place, and size of fish entering the North Equatorial Current. Fish recovered in Hawaii were tagged in April, June, September, October, and November near Baja California, the Revillagigedo Islands, Clipperton Island, and near the boundary of the Equatorial Counter Current and South Equatorial Current at lat 4°N, long 119°W (Table 5). The size-frequency distributions of skipjack caught in the Baja California and Revillagigedo Islands regions presented by Rothschild showed large variation from season to season and year to year. Williams (1972), in another article of this issue, proposes three alternate migration models that explain the recruitment of skipjack into the eastern North Pacific. He concludes that oceanographic conditions in the central and eastern Pacific have a vital controlling effect on the abundance of skipjack in the eastern Pacific fishery.

Finally, year-class strength determined by survival of larvae and juveniles, as suggested by Rothschild, is not ruled out as contributing to the catch rate variations in the Hawaiian fishery. Large interyear differences in oceanographic conditions as reflected by the sea-surface temperatures at Christmas Island (Seckel and Yong, 1971) and the large interyear differences in sea-air interactions observed during the TWZO investigation undoubtedly affect the survival of larvae, as suggested previously, and, therefore, the population size. However, variations of year-class strength of medium and large fish in the Hawaiian fishery may be masked by the effects of varying currents in the eastern and central North Pacific on the distribution of skipjack.

An attractive aspect of the drift hypothesis is its simplicity. Skipjack while in the North Equatorial Current need not do, know, or remember anything other than to search for food. They need not be able to recognize the concentration of salt in the water or distinguish between water types and then know what corrections to make in order to reach the preferred location. They need not be able to recognize time of warming early in the year and then know whether they should or should not enter the Hawaiian fishery. The salinity and temperature indices correlate with availability of skipjack in Hawaiian waters, because the same water motions that affect the distribution of temperature and salinity in the North Equatorial Current (Seckel, 1962) also affect the distribution of skipjack.

In general, it is important to recognize that what is loosely called migration consists of the two components of travel: one resulting from the mean velocity of the water (V_W) and the other from the mean velocity of the fish or fish school relative to the water (V_F). Extreme situations are those where one component is very much smaller than the other so that it can be neglected. There are probably many cases where V_F and V_W are of the same magnitude. An example of these are the migrations of Pacific salmon (Royce, Smith, and Hartt, 1968). During certain times of the oceanic life of salmon, average travel speeds ($V_F + V_W$) of about 6 to 12 miles per day (13 to 26 cm sec^{-1}) are indicated. Ocean currents (V_W) with speeds of only 5 to 10 cm sec^{-1} are therefore of the same mag-

nitude as the mean velocity of the salmon relative to the currents and cannot be neglected. In fact, it is important to consider V_F rather than (V_W + V_F) when studying the navigational abilities or behavior of fish. Even if V_W is one order of magnitude smaller than V_F, when travel times of 1 or 2 years are involved, V_W may not be neglected and the destination will reflect the effect of the current system.

An example of V_W being negligible in comparison with V_F is the travel of albacore across major portions of the North Pacific Ocean. The example where V_F is very much smaller than V_W may be the travel of skipjack from the eastern to the central North Pacific Ocean.

When skipjack reach the vicinity of islands a fixed reference becomes available and the swimming behavior is likely to become different from that in the open ocean. The fish that were tagged by a sonic device near the Hawaiian Islands (Yuen, 1970) are an example of such behavior. The current field is also affected by the proximity of islands. Although the relative magnitudes of the current velocities and swimming velocities may differ from the open ocean case, both velocities must still be considered. The travel behavior of skipjack near islands is, however, a different problem from that considered in this paper because the time scale is in the order of hours rather than weeks.

Finally, the relative magnitude of V_F as compared with V_W may vary throughout the travel history of a particular species of fish. This variation was documented by Royce et al. (1968) for the case of Pacific salmon and may also apply to albacore. Williams (1972) tends to favor "active" migration of skipjack into the eastern North Pacific fishery. Therefore, V_F may not be small when compared with V_W throughout the travel history of skipjack.

CONCLUSION

A plea is made in this paper by way of proposing a model, much as was done by Rothschild (1965), to progress from the exploratory phase of skipjack distribution studies to the experimental phase. Results from exploration (assemblage of data collected without experimental design) were used to demonstrate empirical associations between the availability of skipjack to the Hawaiian fishery and environmental indices. Important to an understanding of the life history is the linkage between environment and the distribution of skipjack that the empirical associations do not provide.

Insight into the linkage mechanisms is gained if the associations are used as leads to hypotheses or models that can be tested experimentally.

Modern technology together with the powerful analytical tools now available make it possible to construct a complete migration-distribution model of skipjack from the eastern and central North Pacific Ocean. In such a model the North Equatorial Current portion would be linked with one of the eastern Pacific models of Williams (1972) and with a larval survival-year class strength model. Swimming velocities of skipjack can be simulated and included in the model. Numerical evaluation of such a model depends upon adequate environmental information, e.g., large-scale sea-air interaction processes, geostrophic and wind-driven velocities of ocean currents.

Important elements that were not discussed in this paper must be evaluated. For example, there are the effects of dispersion on the distribution due to the random motions of skipjack schools and due to large eddies within the current system. Currents, either geostrophic or wind driven, are not necessarily constant within the range of vertical movement of skipjack. The current drift must therefore be tuned to the depth range within which skipjack swim.

The sources for the required environmental information are meteorological observations from ships, that in the future may be supplemented by buoys. Geostrophic current speeds can be monitored by the use of vertical temperature sections obtained from merchant ships regularly traveling specific routes. The dispersive effect of random fish school motions can be determined by using a sonic tag to track skipjack as was described by Yuen (1970). The dispersive effect of eddying currents can be determined from drifting buoys whose positions are monitored by satellite. Predicted drift or progress

of fish schools based on numerical integration can be verified by drifting buoys and by following fish tagged with a sonic device.

The experimental approach will also aid to answer such questions as the following: Why is there little evidence of spawning between the eastern North Pacific and long 140°W? Why are skipjack schools not evident at the sea surface? Is the productivity of the water adequate to support the skipjack schools with a slow net movement? What is the effect of varying forage abundance on the search pattern and therefore the dispersion of skipjack schools?

The implications of an experimental, numerical approach to the skipjack distribution problem are far-reaching. The principal results of the simple drift model used in this paper will hold in a more sophisticated model where observed rather than climatic boundary conditions are used. The results indicate that the probable drift path and concentration of skipjack schools is predictable. Such predictions will increase the harvest efficiency of the skipjack resource. The insight gained into the life history of skipjack, particularly if the survival mechanisms of early life stages are included in the model, will permit elegant management of the skipjack resource.

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SAMPLING ANCHOVY LARVAE WITH A PLANKTON PURSE SEINE[1]

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ABSTRACT

A miniature purse seine (100 ft by 21 ft) was constructed of 333 μ Nitex. It was used in Kaneohe Bay, Hawaii, together with a 1-m plankton net constructed of the same material in order to evaluate the sampling efficiency of the towed plankton net on anchovy larvae (*Stolephorus purpureus*). The results show that during the day, the purse seine is at least an order of magnitude more efficient for larvae over 5.5 mm in length. The largest larva caught by the plankton net was 14.5 mm and by the purse seine 29.5 mm. At night the plankton net was relatively more effective than during the day, catching about 60% as many larvae as the purse seine over the interval 3.5-19.5 mm. The maximum size taken increased to 21.5 mm, but the maximum taken by the purse seine increased to 50 mm. An attempt was made to rationalize the difference between the day plankton net and purse seine catches by a geometric model involving alarm distance and larval swimming speed. The results are moderately satisfactory.

More limited data on anchovy larvae catches by a 10-ft Isaacs-Kidd trawl, ¼-m, ½-m, and 1-m plankton nets are presented and discussed in the framework of the meter net-purse seine data. These analyses suggest one or more paradoxes in the larval escape problem, or that the data are inadequate.

The classical approach to sampling zooplankton is the towed net. This has two disadvantages: an unknown fraction of the organisms in the path of the net escape by dodging and the net integrates the organisms living along a transect of considerable length—making it difficult to consider the catch from a tow as representing an assemblage of coexisting organisms. The dodging problem has been considered by (among others) Fleminger and Clutter (1965) with respect to planktonic crustacea, Ahlstrom (1954) and Isaacs (1965) with respect to fish larvae, and McGowan and Fraundorf (1966) with respect to zooplankton. A general review of the problem is given in UNESCO (1968).

In recent years there have been attempts to apply community theory to the pelagic realms, e.g., Fager and McGowan (1963) and Venrick (1971). Such attempts should involve samples that represent organisms likely to be coexisting. Grab sampling such as used by Venrick (1971) for diatoms is the obvious method of choice as the scale of coexistence can be specified with precision, but existing grab samplers engulf so little water that they are not likely to afford meaningful information on the medium and large zooplankton. The probability that a towed net will integrate several communities has also been recognized and several solutions developed with respect to subdividing a tow, e.g., Longhurst et al. (1966). But if the tow is subdivided small enough for the dimensions to be meaningful, it will not likely strain enough water to sample the less abundant forms.

The purse seine (and other nets of similar design) is an extremely effective large volume grab sampler in wide use by commercial fishermen. Essentially, a wall of net is set in a circle and the bottom closed (pursed) by drawing on the purse lines. This kind of grab sampler can only be effective at the surface and, therefore, is of general application only in shallow water or under circumstances where the surface fauna is of interest.

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The primary purpose of the present study is to evaluate the extent that a large grab sampler (miniature purse seine) can generate samples of fish larvae that are less biased than towed nets with respect to avoidance. The catches of an anchovy larva (*Stolephorus purpureus*) were enumerated from the samples. These were thought to be the most informative of the organisms captured by the net in part because they were present consistently in the samples, in part because they provide a spectrum of small to large zooplankton essentially constant in body form, and in part because there is a wealth of literature on the sampling of fish larvae, in particular, anchovy larvae.

DESIGN AND OPERATION OF THE NET

The net employed was patterned exactly, insofar as operational considerations are concerned, after that described in Hunter, Aasted, and Mitchell (1966), excepting that the body of the net was constructed of 333 μ Nitex.[4] The length of the Nitex section was 100 ft and the depth 21 ft. A small cod end was placed near the bitter end of the net.

The net was usually set in the form of an incomplete circle from a platform mounted on a 16-ft Boston Whaler, so that the net set off the port side. Closure of the circle was effected during the first stages of hauling. The operation from starting the set to pursing generally took less than 5 min. Hauling up the net required 15 to 20 min with two men at work. Figure 1 shows the net in the water at the start of pursing.

All of the data considered in this report were taken in Kaneohe Bay, Oahu, where swell is negligible and seas are generally less than 1 ft. It was tested in open ocean swell and in seas up to 4 ft. The operation was not affected by swell and seemed to be effective in seas of short period waves, although the effect of waves splashing over the float line of the net was not evaluated.

One operational problem that we anticipated never materialized. We had feared that significant amounts of zooplankton would catch on the net as it was being hauled up. This did not happen even in the instance of chaetognaths, apparently because the plankton, being alive, avoided the mesh. During the final stages, it was necessary to carefully wash the catch toward, and finally into, the cod end.

FIELD AND LABORATORY METHODS

The primary objective of the study, comparison of the catches by the purse seine with catches by a meter net, dictated the field sampling pattern. Two skiffs were employed, one with the seine and the other with the meter net. As soon as the seine was set, the second skiff began towing the meter net as close to the seine as possible. The meter net was raised and lowered so as to proportionally sample the same water column fished by the seine. The plankton net was fitted with a Rigosha flow meter. Tows were generally 10 min in duration, but sometimes they were reduced to 5 min when clogging was a problem.

In the laboratory the total wet volume of the samples was measured. The entire sample was scanned for fish larger than 10 mm. Then either the entire sample or an appropriate aliquot was examined in detail, enumerating and measuring all anchovy larvae (*Stolephorus purpureus*), and enumerating anchovy eggs. The entire sample was then reconstructed by appropriate linear adjustments. Finally, all results were adjusted to numbers per 300 m^3. This value was selected because it was intermediate between the actual typical volumes of water strained by the two samplers, giving the advantage that the numbers to be dealt with are roughly the same as the actual numbers of organisms captured.

In all, there were 44 day stations and 10 night stations from Kaneohe Bay. The exact locations of the stations are not relevant to this study and so are not given. Most were made at Tester's stations 1, 2, 5, and 10 (Tester, 1951). Samples were roughly evenly spaced from November 29, 1966, to August 25, 1967.

[4] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

FIGURE 1.—Underwater view of the plankton purse seine just as pursing was initiated. Photograph by Robert R. Harvey.

CALIBRATION OF SEINE

Although, as will be seen later, it is not absolutely necessary for some analyses to know exactly how much water was sampled by the seine, it is desirable to have a reasonably accurate estimate. The size of the net and idealized geometry of a perfect set suggest the net could surround about 500 m^3 of water.

Actual sets are not perfect, and an attempt was made to standardize for obvious imperfections by noting visually estimated percent efficiency during each set. These ranged from 60 to 100% with six from 60 to 65%, nine from 80 to 85%, and the balance (40) from 90 to 100%. All numerical data generated by the samples were adjusted to 100% efficiency.

Since metered plankton net samples were available from presumably the same water as the purse seine, it should have been possible, ideally, to calibrate each set by comparing the catches of some nonmotile component of the plankton, e.g., fish eggs. This was not possible because such items were not consistently present and, more importantly, because high amplitude, short-period patchiness was obviously generating high variability, even between such closely spaced samples.

The final decision was to use total sample volume as a measure of the water strained by the seine, i.e., the volume of water strained by the seine was estimated by comparing the total volume of wet plankton with the total volume of wet plankton taken by the metered plankton net. This was based on the hindsight fact that the volume of non-escapers, e.g., ctenophores, was very large compared with the volume of escapers, e.g., fish larvae, and therefore, the total volume was essentially independent of escapers. Several analytical techniques, e.g., regression, were considered and applied. These yielded estimates of the purse seine volume at 100% efficiency from 305 m^3 to 441 m^3. Finally adopted was a simple comparison of the geometric means (because the volumes were logarithmically distributed) of the two series after raising the meter net catches to 300 m^3 of water strained, and the purse seine catches to 100% efficiency. This yielded a value of 356 m^3 of water strained for the purse seine at 100% efficiency. The procedure was: geometric mean of 54 purse seine catches divided by the geometric mean of 54 300-m^3 plankton net catches multiplied by 300 equals mean purse seine volume of 356. This value, of course, remains an approximation. Any error has no effect on the analytical portions of this paper as the slopes of the length frequency curves are of primary concern. As indicated earlier, the primary purpose of the adjustments is to deal with reasonably real world numbers.

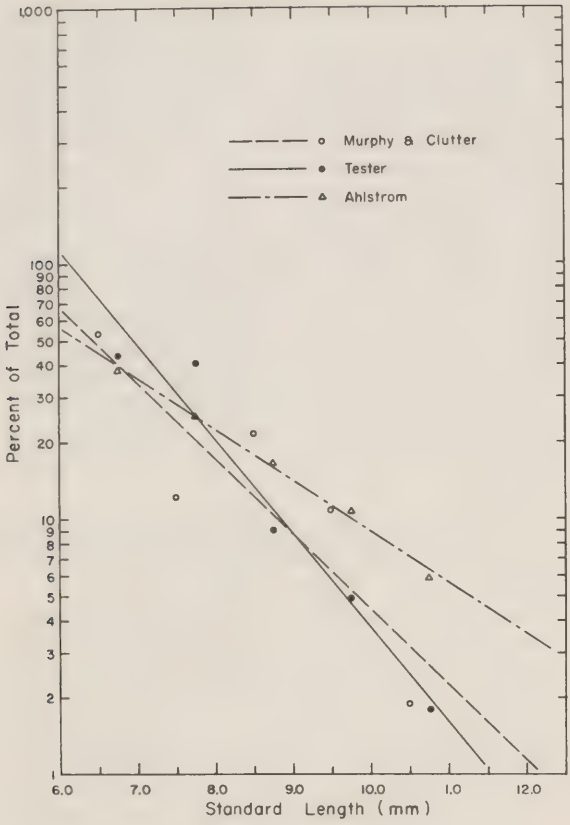

FIGURE 2.—Anchovy larvae catches reported by Ahlstrom (1965) on *Engraulis*, Tester (1951) on *Stolephorus*, and Murphy and Clutter (present paper) on *Stolephorus*. The lines are least square regressions.

RESULTS

DAY SAMPLES

As indicated earlier, the bulk of the sampling was done in the daytime. We used a meter plankton net as our measure of normal sampling efficiency. Because of this, it is of considerable interest to establish how the sampling efficiency of our meter net system compared with the experience of other investigators using the same equipment and towing speeds. This was done by comparing the slopes of our anchovy size-frequency curve with the results of an earlier study in Kaneohe Bay (Tester, 1951) and with the results of a massive program in the eastern Pacific on the northern anchovy (*Engraulis mordax*) (Ahlstrom, 1965).

The results of the three programs (Figure 2) are remarkably similar, and although the *Engraulis* data have a somewhat flatter slope, the difference is not significant, at least for the present purpose. This was not entirely unexpected since the eggs and larvae of *Stolephorus* are almost identical in size and appearance to those of *Engraulis*. We assume that our comparison of purse seine and plankton net catches of anchovy larvae is applicable to all anchovy larvae.

Our day purse seine and meter net data are compared in Figure 3 and Table 1. They indicate remarkable undersampling by the meter net. The break in the slope at 20 mm in the purse seine curve coincides approximately with the transformation from larva to juvenile. This may

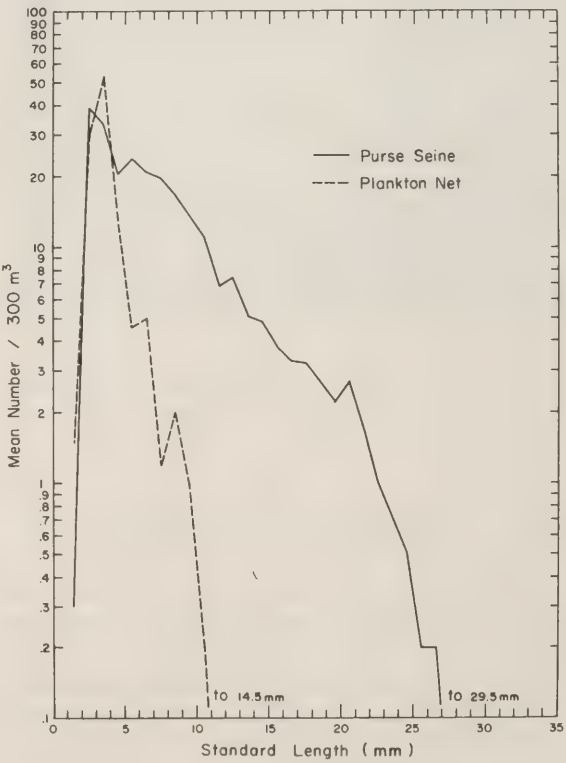

FIGURE 3.—Day catches of the purse seine and plankton net.

TABLE 1.—Results of paired purse seine and 1-m plankton net samples expressed as numbers per 300 m³. Lengths are preserved lengths. There were 44 paired samples.

Standard length (mm)	Day		Night	
	Purse seine	Meter net	Purse seine	Meter net
1.5	0.3	1.5		
2.5	39.3	30.7	13.3	
3.5	33.1	53.9	9.6	6.4
4.5	20.4	13.0	4.6	7.5
5.5	23.6	4.6	10.4	13.3
6.5	20.8	5.0	10.6	6.2
7.5	19.5	1.2	16.4	5.4
8.5	16.6	2.0	18.0	10.8
9.5	13.5	1.0	10.4	14.2
10.5	10.9	0.2	14.0	10.2
11.5	6.9	0.02	17.4	4.2
12.5	7.4	0.05	16.5	6.2
13.5	5.1	0.08	9.0	6.3
14.5	4.8	0.05	5.2	11.0
15.5	3.8		6.1	7.3
16.5	3.3		7.9	4.6
17.5	3.2		2.6	3.5
18.5	2.7		2.6	1.7
19.5	2.2		1.9	1.7
20.5	2.7		2.5	0.3
21.5	1.7		3.4	0.2
22.5	1.0		1.5	
23.5	0.7		1.7	
24.5	0.5		2.0	
25.5	0.2		3.8	
26.5	0.2		5.2	
27.5	0.02		5.6	
28.5	0.03		4.1	
29.5	0.02		2.3	
30.5			4.5	
31.5			1.1	
32.5			1.2	
33.5			1.2	
34.5			0.7	
35.5			1.7	
36.5			0.6	
37.5			0.8	
38.5			0.2	
39.5			0.2	
40.5			0.1	
41.5			0.1	
45.5			0.1	
Total	244.47	113.30	219.9	121.0

be accompanied by behavioral changes, e.g., onset of schooling, as well as more efficient swimming—all of which might increase their ability to escape the purse seine. The low numbers in the 1.0 to 2.0 mm (preserved lengths) are, at least in part, a function of the newly hatched larvae being able to pass through the 333 μ Nitex. The seeming differences in the next two larger intervals are not statistically significant (P = 0.216 and 0.141, respectively). The remainder, involving larvae greater than 4.0 mm, are all significant at the 0.01 level or greater.

NIGHT SAMPLES

The night samples (Table 1, Figure 4) were fewer in number (10) and, therefore, exhibit greater variance. They also suffer from poor stratification as evidenced by the near lack of a negative slope below 12 mm in length, in spite of what must be a very high mortality rate (see Figure 3). These data clearly indicate that the purse seine is superior at night too, even with respect to the smaller sizes, supporting Ahlstrom's (1954) contention that larvae probably dodge nets at night as well as day. For example, over the interval 3.5 to 11.5 mm, inclusive, the purse seine took 127.9 per 300 m³, and the meter net took only 69.8. Over a larger interval (3.5-19.5 mm), the purse seine took 163.2 larvae and the meter net 99.6. For this interval the F ratio is 6.19 with 1 and 32 df ($P < 0.025$). Never-

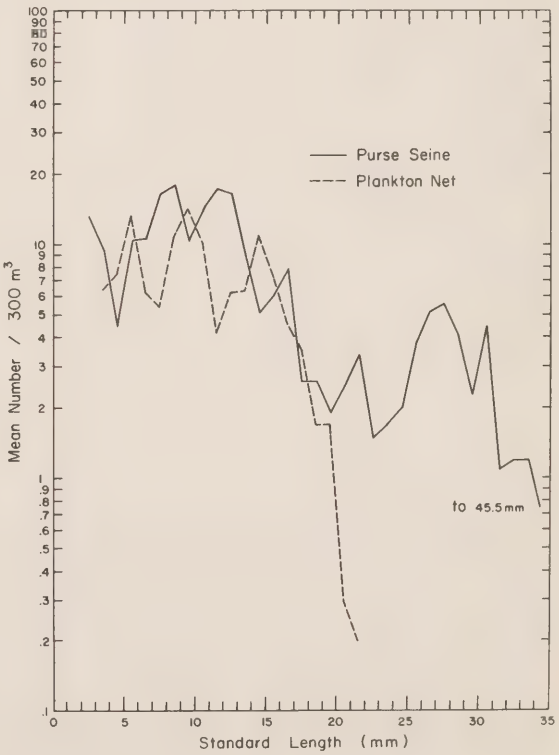

FIGURE 4.—Night catches of the purse seine and plankton net.

theless, the plankton net appears to be more efficient at night than during the day. The catches of the smaller larvae are closer to the purse seine catches than during the day, and much larger larvae were taken at night—21.5 mm maximum versus 14.5 mm by day. This suggests that vision plays an important role in dodging.

It is interesting to note that the maximum size taken by the plankton net at night (21.5 mm) coincides with a change of slope of the day purse seine catches. The plankton observation taken by itself might be interpreted as a size beyond which all larvae can swim out of the net even if they blunder into it. A length of 21.5 mm is approximately the size of metamorphosis and the onset of schooling. This social trait might also adversely affect the day purse seine catches to the extent that a school is more effective than the sum of the individuals in detecting and responding appropriately. It does not seem to have affected the night catches. This may be evidence that schools tend to disperse at night.

Each night station was paired with a day station. These latter were taken late in the afternoon at the same geographical point, but of necessity, several hours before the night station. Examination of the data shows that this degree of control was inadequate to allow meaningful comparisons, at least on the basis of only 10 sets of data.

A DODGING MODEL

In this section an attempt is made to rationalize the difference between the day plankton net catches and the day purse seine catches on the basis of the geometry of the towed net situation, the swimming speed of the larvae, and the alarm distance, i.e., the distance in front of the net that a larva would have to begin evasive action in order to avoid capture.

The algebra of the model is an extension of the results of Barkley (1964). We start with his equation (7) (our 1) which defines the escape velocity, i.e., swimming speed, necessary to escape a net assuming the larva is mathematically inclined and rational and, therefore, selects the shortest possible escape path. We follow Barkley's notation.

$$u_e = U\left[1 + \frac{x_0^2}{(R - r_0)^2}\right]^{-1} \quad (1)$$

where: u_e = escape velocity (swimming speed) (cm/sec)
U = towing speed of net (cm/sec)
x_0 = reaction distance of the larva (cm)
r_0 = initial offset of larva (from dead center of the net) (cm)
R = radius of net (cm).

Equation (1) can be rearranged to provide the minimum r_0 from which escape is possible given a swimming speed u_e yielding:

$$r_0 = R - [x_0 u_e (U^2 - u_e^2)^{-1}]. \quad (2)$$

Of course, escape is possible from all larger r_0's.

Now the proportion that escapes (P) is from elementary principles:

$$P = (\pi R^2 - \pi r_0^2)(\pi R^2)^{-1} \quad (3)$$

Substituting the right hand side of (2) into (3) and rearranging yields the desired equation, i.e., an expression relating the proportion escaping to swimming speed and alarm distance as follows:

$$P = \left[R - \left(\frac{x_0 u_e}{U^2 - u_e^2}\right)\right]^2 R^{-2}. \quad (4)$$

From (4) we can define the proportion caught (P') as simply $1 - P$. Assuming that the purse seine catches all larvae up to 10.5 mm by day, the proportion caught (or escaping) can be estimated as a function of size. The towing speed of the net was about 1.5 knots (76 cm sec^{-1}). This leaves two unknowns, alarm distance (x_0) and swimming speed (u_e). Our approach in testing the model is to estimate swimming speed as a function of size based on values in the literature, and solve for alarm distance—also as a function of size. As will be seen, the derived alarm distances seem intuitively reasonable and, anticipating a later section, may explain the relatively small increase in sampling power of larger towed nets.

Appropriate measurements on the swimming speed of larval anchovies are not available. What

are required are maximum sustainable speeds over distances ranging from 0 to 100 cm or so. Houde (1969) found that yellow perch larvae larger than 9.5 mm could sustain speeds up to 4 body lengths per sec for 1 hr. Larimore and Duever (1968) observed swimming speeds over 10 body lengths per sec for over 3 min for smallmouth bass 20-25 mm in length. Hunter and Zweifel (1971), Figure 4, present data for sustained swimming of jack mackerel 4.5-27.0 cm for short periods. These data fitted to the expression $y = ax^b$ yielded an a of 18.06, b of 0.829, and r of 0.997, y being speed in centimeters per second, and x body length (L) in centimeters. This gives an extrapolated speed of 10 cm per sec for a 5-mm nehu larva. More recently, Hunter (1972) observed burst speeds of very short duration as high as 28 lengths per sec for a 4.2-mm larva and 25 lengths per sec for a 12.1-mm larva. Whether such speeds can be sustained long enough to explain plankton net avoidance is not known. In the computations to follow, we assume that they can be sustained as follows. One trial (u_e') assumes that the backward extrapolation of the data by Hunter and Zweifel (1971) holds (cm/sec = $18.06\ L_{cm}^{0.829}$), and the second trial (u_e'') assumes that cm/sec equals body length in centimeters times 10.

The catch data were processed as follows. The raw data (second and third columns in Table 2) were fitted to exponential expressions (fourth and fifth columns). The purse seine data were then multiplied by 46.883/29.685 to adjust the data to the point of assumed 100% meter net efficiency (see Figure 2). P', the fraction retained, was then calculated as $1 - P$. u_e' and u_e'' were then calculated from the expressions in the preceding paragraph. Minimum alarm distance, x_0, was then calculated from:

$$x_0 = \frac{R\,(U^2 - u_e^2)^{1/2}\,[1 - (P')^{1/2}]}{u_e} \qquad (5)$$

which is a straightforward rearrangement of equation (4). The resulting minimum alarm distances (last two columns in Table 2) do not seem unreasonable. For example, it seems reasonable that a 7.5-mm larva could detect a meter net 200-400 cm away and begin to take meaningful evasive action. The greater effectiveness of towed nets at night might be caused by a reduction in detection distance as well as reduced ability to take early, well-directed evasive action.

OTHER TOWED NETS

Two additional sets of data will be considered here. The first is a comparison between a 10-ft Isaacs-Kidd trawl and a standard meter net. The ratio of mesh area-to-mouth opening was the same for both nets in order to ensure comparability of hydrodynamic and clogging characteristics. The trawl was meshed throughout with Nitex having an opening of 0.505 mm. This is nearly the same as that used in the standard CalCOFI (California Cooperative Oceanic Fisheries Investigations) meter net which, according to Smith, Counts, and Clutter (1968), had silk gauze with a mesh width of 0.55 mm as its main

TABLE 2.—Calculation of escape parameters for meter net and purse seine data.

Standard length (mm)	Purse seine observed	Meter net observed	Purse seine calculated[1]	Meter net calculated[2]	Purse seine adjusted[3]	P'	u_e'*	x_0'†	x_0''†
3.5	33.082	53.905	29.685	46.883	46.883	1.000	7.564	0	0
4.5	20.366	12.984	26.063	19.754	41.163	.4799	9.316	134.7	288.7
5.5	23.575	4.627	22.883	8.323	36.140	.2303	11.002	190.6	397.0
6.5	20.807	5.048	20.091	3.507	31.731	.1105	12.637	210.3	428.1
7.5	19.507	1.157	17.639	1.478	27.858	.0531	14.228	212.6	424.6
8.5	16.616	2.048	15.847	.623	25.028	.0249	15.7837	207.0	407.0
9.5	13.457	1.034	13.597	.262	21.474	.0122	17.3082	196.9	381.8
10.5	10.941	0.018	11.938	.111	18.854	.0059	18.8054	185.6	355.8

[1] P.S. $Y = ae^{bx}$ $r = -.93779$ $b = -.13013$ $a = 46.81074$ x = length (mm).
[2] M.N. $Y = ae^{bx}$ $r = -.90039$ $b = -.86431$ $a = 965.5874$ x = length (mm).
[3] P.S. calculated × 46.883/29.685.
* $u_e' = 18.06\ L\ (\text{cm})^{0.82896}$; $u_e'' = 10\ L$ (cm).
† $x_0 = \dfrac{R\,(U^2 - u_e^2)^{1/2}\,[1 - (P')^{1/2}]}{u_e}$.

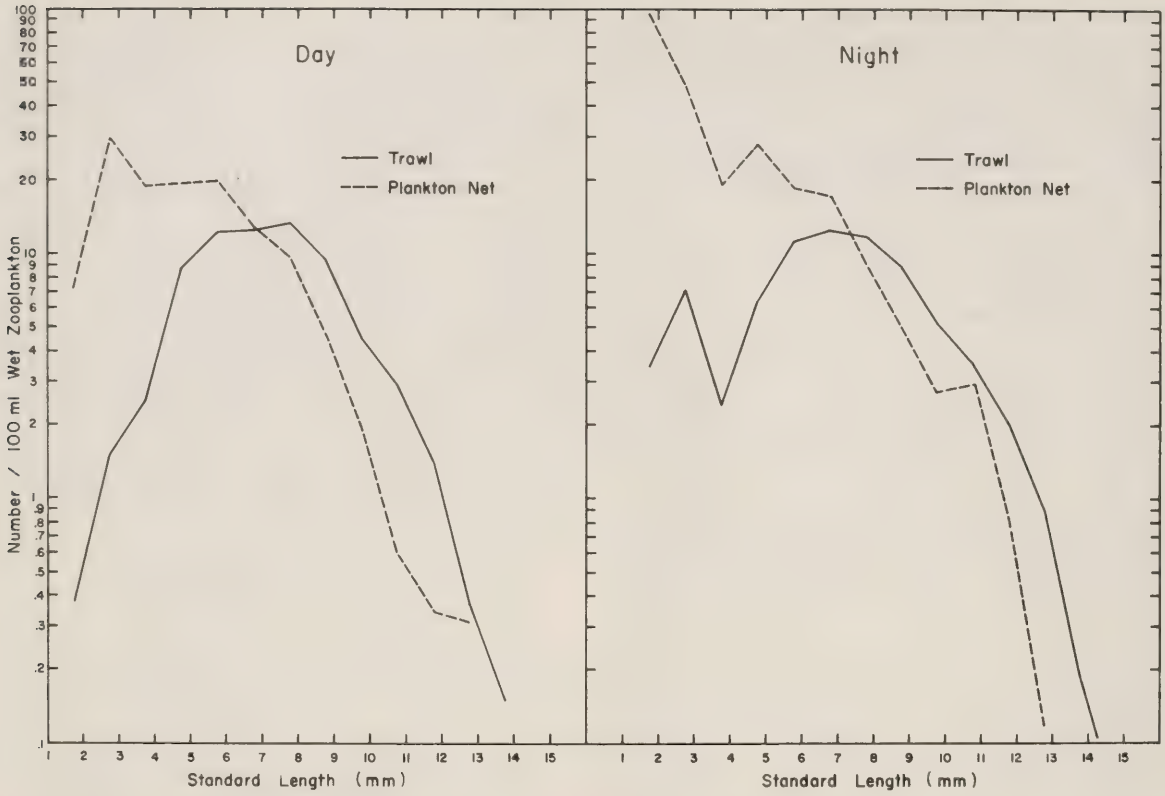

FIGURE 5.—Day and night catches of the Isaacs-Kidd trawl and the standard CalCOFI meter net.

body. It had a porosity of 36% after use compared to 51% for the Nitex. For this reason, the trawl, though preserving the geometry of the meter net, has a slightly better filtering capacity. These two nets were alternated over replicate courses off southern California during the period May 6 to May 8, 1964. In all, there were 22 paired day samples (½-hr tows) and 10 paired night samples.

The trawl-plankton net series are compared in Table 3 and Figure 5. The results are expressed as numbers per 100 ml of wet plankton taken. This was thought to be the best way to control the catches between the unmetered trawl and the metered plankton net. The severe undersampling of the small larvae by the trawl has no ready explanation, but could have been caused by our inadvertently having to tow at a faster speed in order to maintain the vaned trawl at proper towing depths or by the greater transparency of the Nitex, which would reduce the effect of partial clogging on effective mesh size. The trawl is about twice as effective as the plankton net (Table 3) in the capture of larvae over 8.75 mm in length by day, but only slightly more efficient at night. With respect to both day and night, the trawl falls far short of the purse seine both with respect to the increased catches of larger larvae and the extension of upper limit of capture. The latter, of course, might be ascribable to the absence of larger larvae at the California sampling stations, but this seems unlikely.

The mean escape radius for the trawl is 3.4 times that of the meter net and led us, a priori, to expect a much greater enhancement of the

TABLE 3.—Summary of the meter net and trawl catches of anchovy larvae off southern California, May 6-8, 1964. The data are in numbers per 100 ml of wet volume zooplankton taken.

Length (mm)	Day		Night	
	Meter net	Trawl	Meter net	Trawl
1.75	7.332	0.382	96.160	3.490
2.75	28.746	1.491	48.030	7.110
3.75	18.869	2.473	19.360	2.430
4.75	19.320	8.619	28.060	6.410
5.75	19.927	12.222	18.880	11.200
6.75	12.860	12.578	17.130	12.480
7.75	9.646	13.168	9.070	11.890
8.75	4.650	9.432	5.020	8.880
9.75	1.959	4.537	2.760	5.260
10.75	0.604	2.887	2.960	3.590
11.75	0.345	1.428	0.840	2.020
12.75	0.313	0.368	0.120	0.900
13.75	--	0.150	--	.190
14.75	--	--	--	.060

TABLE 4.—Catches of four replicates of the purse seine and three simultaneously towed nets. Numbers are per 300 m^3 of water strained.

Length (mm)	Purse seine	1-m net	½-m net	¼-m net
2.5	1,289.8	689.3	278.6	95.7
3.5	296.6	1,122.7	686.2	217.9
4.5	156.8	152.0	67.9	35.8
5.5	81.0	20.6	26.7	8.2
6.5	135.4			
7.5	89.5			
8.5	129.5			
9.5	49.3			
10.5	31.1			
11.5	29.6			
12.5	25.3			
13.5	41.4			
14.5	9.3			
15.5	10.1			
16.5	17.4			
17.5	2.6			
18.5	1.7			
19.5	6.9			
20.5	10.9			
21.5	7.8			
22.5	10.1			
23.5	8.3			
24.5	4.9			
25.5	0.9			

catches. Perhaps the larger size is detected farther away (increased x_0), cancelling most of the advantage. This suggests that a towed net has to be large enough not to be perceived as a meaningful whole in order to significantly increase the catches of efficient escapers such as the anchovy.

The final set of data to be considered is four sets of stratified (in the same way as the purse seine-meter net data) samples taken by purse seine, 1-m net, ½-m net, and ¼-m net. All four sets were obtained on August 25, 1967, during daylight. The results (Table 4), apart from again demonstrating the superiority of the purse seine, are somewhat ambiguous. The towed nets clearly show a dramatic decrease in efficiency with decreasing size in terms of numbers caught, but the also-to-be-expected increase in slope (negative) with decreasing net size is not apparent.

The total numbers caught by the three towed nets are approximately proportional to the mean escape distance, but this observation is at variance with the slight improvement associated with the 10-ft trawl compared to the meter net discussed earlier. Very possibly the inconsistencies are a function of the limited sampling, especially with respect to this last set of data.

DISCUSSION

Clutter and Anraku (1968) thoroughly reviewed the dodging problem on the basis of evidence and literature then available. Many of the data they reviewed were contradictory, and to some extent, we have extended the library of contradictions in this paper. We have, however, clearly shown from our purse seine data that towed nets are rather inefficient as samplers of at least one kind of fish larvae (anchovy)—especially by day. Likely, this conclusion can be extended to other pelagic larvae, as there must surely be strong selective pressure for avoidance of predation.

The algebraic model developed to reconcile the difference between our day purse seine and meter net catches involved two parameters, escape speed and alarm distance. It may be that future experimental work will not sustain the assumed escape velocities. If not, either a new model must be invoked or the alarm distance must be increased. The transparency of the water in Kaneohe Bay is low, so a very great extension of alarm distance on the basis of vision is not intuitively attractive.

A great deal of work has been directed at the design of towed nets in order to clean them up with respect to their disturbance in the water

and, hence, the vigor with which they telegraph their arrival. Yet, the dramatic improvement in the efficiency of towed nets at night suggests that vision is the most important avoidance cue. But, the optical characteristics of sea water are such that objects become invisible through contrast attenuation rather than resolution attenuation. This being so, large nets such as the Isaacs-Kidd trawl should be sighted at nearly the same distance as smaller nets such as the meter net. There should, then, be a dramatic increase in effectiveness with size. This is not evident in our data or anyone else's.

Short of resolving these contradictions, it appears that the development of towed sampling devices should proceed, as suggested by Clutter and Anraku (1968), in the direction of larger size, greater speed, and invisibility. The large scale "grab" sample, of which our purse seine is a rather specialized example, appears to be a possible definitive solution, or at least a practical means of calibrating towed nets.

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SELECTIVITY OF TOWED-NET SAMPLERS

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ABSTRACT

The ideal sampler for plankton and nekton is one whose selective characteristics are known to be appropriate to any given problem, so that it catches the right organisms, and rejects others, with known efficiency. This paper presents a quantitative theoretical analysis of one aspect of selectivity, avoidance of towed-net samplers. The theory is evaluated against three sets of paired samples obtained by different nets at different speeds to provide absolute and relative tests of its validity. A single sample obtained by one net towed at one speed is then analyzed to illustrate the procedure. Final evaluation of the theory awaits studies of animal behavior when confronted by a sampler, but the theory provides informative and reasonable interpretations of plankton and nekton catch data, particularly estimates of population abundance and mesh losses, even when behavior of the animals is not known.

An ideal sampler for plankton and nekton must meet at least two requirements, one qualitative and the other quantitative: It must collect or detect certain components of these extremely diverse communities, while rejecting most others; and it must do this with known effectiveness. For some purposes the qualitative aspects of sampler selectivity are relatively more important than the quantitative ones, or vice versa, but neither can ever be completely ignored in the design and selection of sampling gear.

Sampler selectivity has usually been evaluated empirically, by comparing results obtained with one sampler under different conditions or by intercomparing various sampling methods. The plankton purse seine developed by Murphy and Clutter (1972) appears to be nearly ideal for the latter purpose. It is relatively nonselective for a wide spectrum of organism types and sizes, making it useful as a "primary standard" for calibrating more selective gear, as Murphy and Clutter demonstrate.

A sound theory of sampler selectivity would be of great value as a guide to the collection and analysis of empirical data, but relatively little effort has been devoted to the development of such theory (Tranter, 1968). What I propose to discuss here is a special, rather basic, case of selectivity: the theoretical minimum probability of certain capture, for many individual encounters between similar organisms and a towed-net sampler.

The formulation of this problem was suggested by the work of Murphy and Clutter (1972). The results resemble those obtained by Gilfillan (reported by Clutter and Anraku, 1968) but are more general. This study is an extension of my earlier theoretical work on net avoidance (Barkley, 1964) and uses the same notation.

This paper is presented in recognition of the inspiration and leadership of Oscar Elton Sette. It is appropriate that it should appear just one century after the first worldwide use of the Müller net on the *Challenger* Expedition.

METHOD

Consider a towed-net sampler moving through the water toward an individual animal (Figure 1a); for simplicity assume that the net has a circular opening of radius R and moves at a constant speed U. The animal senses the oncoming net and begins to react to it at a distance x_0, by swimming at some mean escape speed u_e. In the time available before the net catches up, the animal either can, or cannot, get out of the way, depending on its position, speed, and di-

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rection of movement relative to the net. There is, therefore, a cone-shaped space ahead of the net which, once it encloses the animal, results in certain capture. If the animal reacts before entering the (invisible) "lethal cone," it has enough time to get out of the way of the oncoming net. The base of this "lethal cone" is the opening of the net; its apex is at a distance X ahead of the net. This distance, X, is given by the equation:

$$X = R\sqrt{\frac{U^2}{u^2_e} - 1} \qquad (1)$$

which is easily obtained from the following equation (Barkley, 1964) by setting $r_0 = 0$ and $x_0 = X$:

$$u_e = \frac{U}{\sqrt{1 + \frac{x^2_0}{(R - r_0)^2}}} \qquad (2)$$

Figure 1 (panels a and b) gives examples of the "lethal cone" for several values of escape speed relative to net speed. For organisms which do not react to the net ($u_e = 0$) or have very low escape speeds the "lethal cone" is very large, occupying all or almost all of the volume of water in the path of the net; the probability of capture for such organisms approaches 1.0. On the other hand, for animals whose escape speed approaches the speed of the net ($u_e \simeq U$) the "lethal cone" is short; these animals can easily dodge the oncoming net, even if they wait

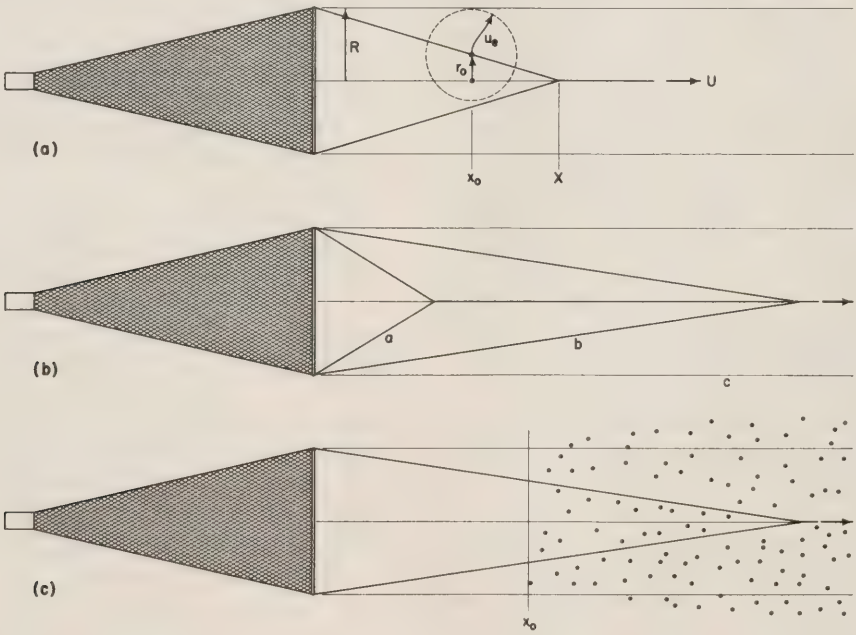


FIGURE 1.—(a) An animal at a point x_0 ahead of the net and r_0 from its axis of motion begins to react to the net. In the time available, it can go anywhere within the volume shown in dashed lines; if this volume is completely enclosed by the oncoming net, capture is certain. Animals which react before entering the cone-shaped space ahead of the net can escape; those which react after entering the "lethal cone" are caught. (b) For a given net, the length of the "lethal cone" depends only on the speed of the animal relative to the net. Cone a corresponds to animals which can move at 50% of the net's speed. Cone b represents a relative speed of 15%; cone c shows the case of no reaction. The "lethal cone" in panel a, above, corresponds to a relative speed of 30%. (c) If a school or cluster of animals reacts to the dodging movements of the animals nearest the oncoming net, only those animals already inside the "lethal cone" are certain to be captured.

until the net has almost caught up with them. We do not expect to catch any animals which can swim faster than the net; we wish to calculate minimum probabilities for certain capture, which implies that animals which could possibly escape do so. That is, the size of the "lethal cone" is minimized by assuming that animals are capable of optimum avoidance behavior.

However, probabilities of certain capture can only be calculated for animals which react individually. Animals which school or form clusters can "beat the odds" by reacting to each other's behavior instead of reacting only to the oncoming net. The effect of this is illustrated in Figure 1c, which represents a net approaching a group of animals whose reaction distances and escape velocities are assumed to be similar. If the animal shown nearest the net begins to react at the distance labeled x_0, it can escape because it is outside of the "lethal cone." Those animals already within that cone will be captured in any case. If the other animals respond immediately to the actions of the one nearest the net, they can all escape. If, instead, they respond as individuals, as the net moves through the group, more will enter the "lethal cone" and then be captured.

Whether an organism, once captured (i.e., enclosed by the net) will be retained depends on the characteristics of the net's meshes and the size, shape, behavior, and fragility of the organism. Losses through the mesh have been reviewed by Heron, 1968; Tranter and Smith, 1968; and Vanucci, 1968. Lenarz (1972) presents results of more recent work. Losses can also occur due to faulty handling of the sampler, particularly sudden decreases in towing speed. Our primary interest here is in avoidance prior to capture, although the theory to be developed will throw some light on the problem of mesh losses.

The catch obtained from a towed-net sampler can be calculated, in principle, from equations such as the following:

$$\text{Catch} = \text{Captures} - \text{losses}$$

$$= (\text{volume sampled}) \times \left(\frac{\text{no. of organisms}}{\text{unit volume}}\right) \times (\text{probability of capture}) - (\text{losses}) \quad (2)$$

So that

$$\frac{\text{no. of organisms}}{\text{unit volume}} = \frac{(\text{catch} + \text{losses})}{(\text{volume sampled}) \times (\text{probability of capture})} \quad (3)$$

The central problem of selectivity theory is to evaluate the unknown factors in equations (2) and (3), so as to permit solution of these equations with a minimum of empirical work. The most important unknown factors are those governing probability of capture and losses after capture—primarily losses through the meshes.

Since both probability of capture and degree of mesh loss must vary widely with species, age, and condition, the above equations apply separately to each component of the plankton and nekton community.

For present purposes, a component must be defined as a set of organisms having the same probability of capture, and the same degree of mesh retention, under given circumstances. That is, they must be similar in their reaction distance, escape speed, shape, size, and condition.

The above operational definition of a component of the plankton or nekton may often coincide with the more usual biological definitions. For single species, one can reasonably expect that fish of similar size or crustaceans at the same stage of development should have similar reaction distances and escape speeds and the same percentage mesh retention. However, the distinction between the two ways of defining a component must be carefully borne in mind. The operational definition may lump several biologically defined components; to take a trivial example, bacteria, phytoplankton, and fish eggs small enough to pass through the mesh all have the same probability of capture, 1.0, and all have 0% retention. On the other hand, the operational definition may split one biological component into two or more parts; e.g., healthy and moribund animals of the same size and species should differ in their ability to avoid capture. In principle, empirical data on reaction distance,

escape speed, shape, size, and condition are needed to assign animals to different components when analyzing towed-net samples by means of the present theory. Such data could perhaps best be obtained by taking stereoscopic photographs of animals' reactions to the approach of a sampler. In practice, however, it may be possible to assign animals to operationally defined components *post facto*, based on analyses of catch data with the present theory. An example of this is to be found in Table 1, where *Bathylagus stilbius* ranging from 52 to 92 mm in length were found to have essentially identical probabilities of capture and were apparently all retained by the meshes, thus meeting the criteria for a single component.

In equations (2) and (3) the major unknowns are the losses and the probability of capture. Neither can be formulated precisely until behavior of many animals, before and after entering nets of varied designs, has been studied. However, losses can be estimated to some degree from the difference between observed and theoretical catches; and probability of capture can be calculated for a limiting case, minimum probability of certain capture for individual encounters. This approach makes use of the geometry of the "lethal cone" (Figure 2). The minimum probability of capture, P_c, is:

$$P_c = \frac{\text{Area of "lethal cone" cross section at distance } x_0}{\text{Area of the sampler mouth opening}} = (r/R)^2.$$

From Figure 2,

$$\frac{R - r}{x_0} = \tan \alpha = \frac{R}{X}$$

so that

$$r = R\left(1 - \frac{x_0}{X}\right)$$

and

$$P_c = \left(1 - \frac{x_0}{X}\right)^2. \tag{4}$$

Substituting X from equation (1) into (4) gives

$$P_c = \left(1 - \frac{x_0}{R\sqrt{\frac{U^2}{u_e^2} - 1}}\right)^2 \tag{5}$$

which may also be written

$$P_c = \left(1 - \frac{x_0 u_e}{R\sqrt{U^2 - u_e^2}}\right)^2 \tag{6}$$

Where P_c is probability of capture, x_0 is the mean reaction distance, R is the radius of the net's opening, U is the net's speed, and u_e is the animals' mean escape speed. These results can also be derived from equations (4), (5), and (7) of my earlier analysis (Barkley, 1964).

DISCUSSION

To examine avoidance as a function of towing speed, Gilfillan (reported by Clutter and Anraku, 1968) assumed that the product $x_0 u_e$ is a constant, K. Starting with an apparent "effective"

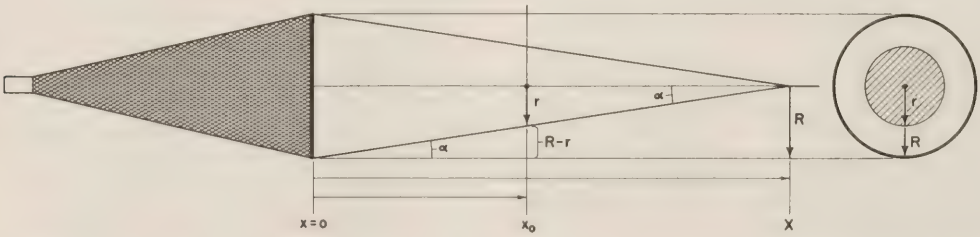


FIGURE 2.—Definition sketch for calculating P_c, the minimum probability of capture. P_c is the ratio of the area of the "lethal cone" (shaded) to the area of the net's mouth opening, at the mean reaction distance x_0 for one component of the catch.

net radius R' (identical with r in Figure 2), Gilfillan arrived at the following equation:

$$P_c = \left(1 - \frac{K}{RU}\right)^2, \qquad K = x_0 u_e \quad (7)$$

where present notation has been substituted for the original and the equation slightly simplified. Clearly Gilfillan's equation is an approximate form of equation (6) for the case where u_e can be neglected compared to U; which is to say, for animals which move much slower than the net. This approximation is good to within 5% as long as u_e is less than 30% of U.

It is not obvious that $x_0 u_e$ should in general be a constant, even for a single component of the plankton or nekton. Constancy of the product $x_0 u_e$ implies that either (1) reaction distance and escape speed individually are constant, (2) animals deficient in one of these survival traits can compensate for this by excelling in the other, or (3) animals given an unusually long time to react by faulty net design—such as a bridle or other conspicuous obstruction some distance ahead of the mouth—fail to take advantage of this warning. The first alternative is perhaps too much to expect; the second and third seem unlikely. Nevertheless, Gilfillan obtained nearly constant values for K in a series of field trials with different nets towed at various speeds, where catches of *Calanus* spp., *Euchaeta japonica*, and euphausiids were enumerated (Clutter and Anraku, 1968).

There is great practical value to knowing that K is a constant for any particular component of a sample, because this constant fully specifies the avoidance behavior of that component. If K is constant, it is possible to calculate probabilities of capture without making measurements of either x_0 or u_e, as long as U is known to exceed u_e by a factor of three or more.

Numerical values of K can be estimated, as Gilfillan suggested, from tows made at two different speeds, U_1 and U_2, or by using two otherwise similar nets with openings of radii R_1 and R_2, while holding other factors constant:

$$K = \frac{1 - \left(\frac{C_1}{C_2}\right)^{1/2}}{\frac{1}{R_1 U_1} - \frac{1}{R_2 U_2}\left(\frac{C_1}{C_2}\right)^{1/2}} \quad (8)$$

where C_1/C_2 is the ratio of catches of individual components in the samples taken under each of the two different conditions. Equation (8) is approximate; the exact form can be obtained by substituting $\sqrt{U^2_n - u^2_e}$ for U_n.

Holding "other factors" constant is obviously a problem, since the same net towed at different speeds, or different size nets towed at the same speed, may have widely different noise levels, mesh losses, hydrodynamic behavior, etc., which would tend to invalidate the comparison.

RESULTS

Although definitive tests of the theory developed above must await knowledge of avoidance and mesh escape behavior of at least some components of the plankton and nekton, a few informative comparisons can be made now between theory and catches obtained with various towed nets.

Equation (5) is presented graphically in Figure 3, where P_c, the minimum probability of capture (ordinate) is plotted as a function of the ratio u_e/U, the escape speed relative to the net's speed, for various values of the ratio x_0/R, the reaction distance relative to the net's radius. The linear graph shows the complete theoretical solution; it is used to provide a check on results obtained using the semilog format. In practice the semilogarithmic graph is more useful for analyzing catch data because it simplifies graphical calculations. Either of these graphs, as well as equations (5), (6), and (7), can of course be used to determine P_c, u_e, or x_0 if any two of these variables are known, along with R and U. For example, a 1-m net ($R = 0.5$ m) towed at 100 cm/sec should catch at least one-third ($P_c = 0.33$) of all those organisms in its path which react at a distance of 1 m and can swim 20 cm/sec ($u_e/U = 0.2$, $x_0/R = 2$).

A more interesting application is the use of Figure 3 to analyze size-frequency data from a tow, or set of tows, made with one sampler at one speed. To illustrate this application, suppose that the population in question is a species for which mesh losses are negligible beyond some

minimum size or stage of development and that the species' abundance does not change appreciably with size, or that corrections can be made for these two factors. Assume that the species' swimming ability is known, and proportional to size, while its reaction distance remains constant, or nearly constant, for all sizes sampled. Then if the catch were sorted into size class intervals (ideally, into components, in the operational sense) and counted, the size classes could each be assigned a corresponding escape speed, increasing with size; plotting these speed-frequency values as points on either graph of Figure 3 would produce a curve which resembles one of the family of curves shown on those graphs. Proper matching of observed data to the theoretical curves would yield unique values of both P_c and x_0/R (and therefore x_0, since R is known) for each component or class interval of that species. Once P_c is known, the absolute population density can be calculated from equation (3). Finally, values of x_0, or x_0/R, provide valuable information as to the relative merits of different sampler designs.

The following examples illustrate this use of avoidance theory. In the first example, the population density structure is known, so that P_c can be calculated directly and only x_0 remains to be determined from avoidance theory. In the second example, two different samplers are compared to obtain estimates of P_c and x_0 for both. from the theory, even though the population structure is not known. The third example illustrates information which can be obtained when one sampler is towed at two different ranges of speed. Finally, catch data from a single net, towed at one speed, are considered.

Murphy and Clutter (1972) present length-frequency data for Hawaiian anchovy, the engraulid, *Stolephorus purpureus,* caught with their plankton purse seine and a 1-m net. Their data for paired daylight tows are reproduced on Figure 4. The uppermost curve on this figure shows length-frequency data from the purse seine, assumed to represent the population structure as a function of size. I approximate these data by means of the straight line shown on this figure, in effect assuming that the population declines exponentially as the fish grow to larger sizes. That is, $N_L = N_0 \exp(-kL)$, where N_L is the population density at length L, N_0 is a fictitious population density at zero length obtained by extrapolation, and k is a constant. The lowest curve on Figure 4, marked C_L, shows the catch (C) in each 1-mm length class (L).

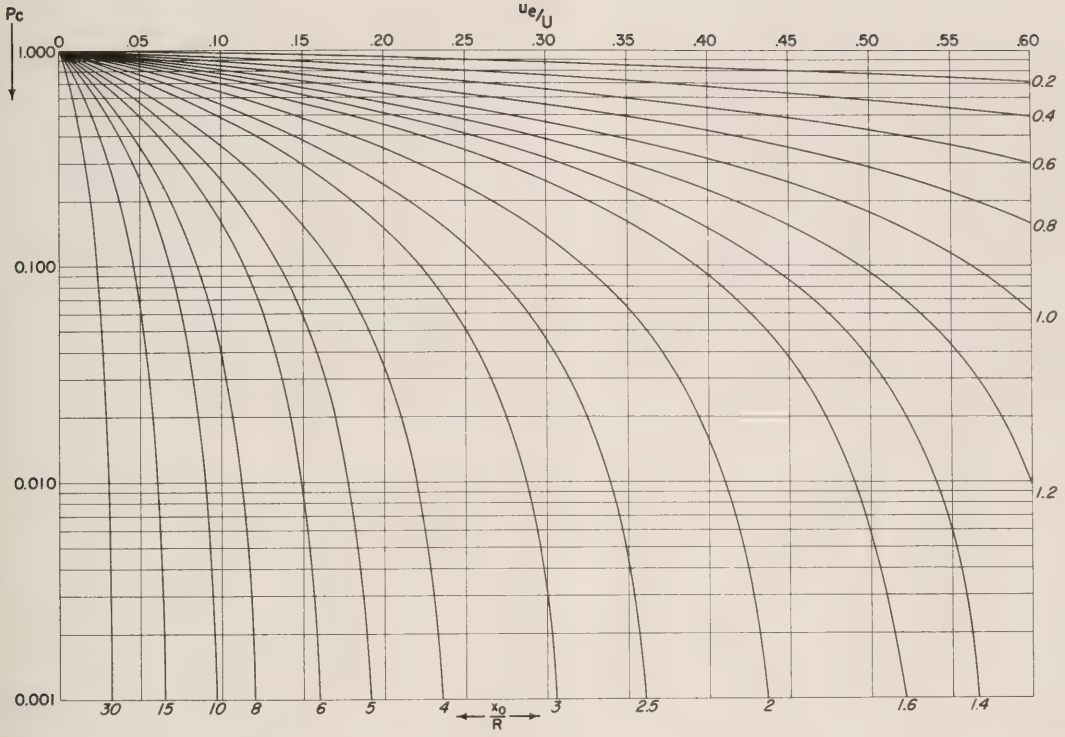
To remove the effects of changes in population density, set $N_0 = 1.0$ by dividing all values of N_L by the population density at N_0. On semilog graph paper this can easily be accomplished simply by aligning N_0 with 1.0 on the ordinate scale, after the length-frequency values have been plotted on tracing paper using the three-cycle semilog scale of Figure 3. Next, divide each value of C_L by the corresponding value of N_L to obtain the middle curve of Figure 4, labeled C_L/N_L. This division can be performed graphically by moving each value of C_L vertically upward a distance equal to the vertical distance between N_L at the corresponding length, L, and the horizontal line $P_c = 1.0$. This procedure yields the length-frequency curve which would have been obtained if the population density in each class interval had been the same, i.e., $N_L = N_0$.

The above procedure amounts to dividing catch per unit volume by the population per unit volume, which according to equation (2) yields

$$\frac{\text{Catch/unit volume}}{\text{No. of organisms/unit volume}} = \text{Probability of capture (if losses} = 0).$$

Thus the curve labeled C_L/N_L on Figure 4 is also a curve showing P_c for each class interval, providing that catch per unit volume has been correctly related to the population per unit volume in each class interval and that mesh losses are negligible.

Mesh losses appear to be negligible for animals larger than the two smallest class intervals, which will not be used in the analysis. Since u_e is not known, length for each class interval is converted to escape velocity by assuming that $u_e = 10L$ where u_e is in cm/sec and L is in cm. Each value thus obtained is divided by U, nominally 76 cm/sec. Resulting values of u_e/U are shown in the upper abscissa of Figure 4. The



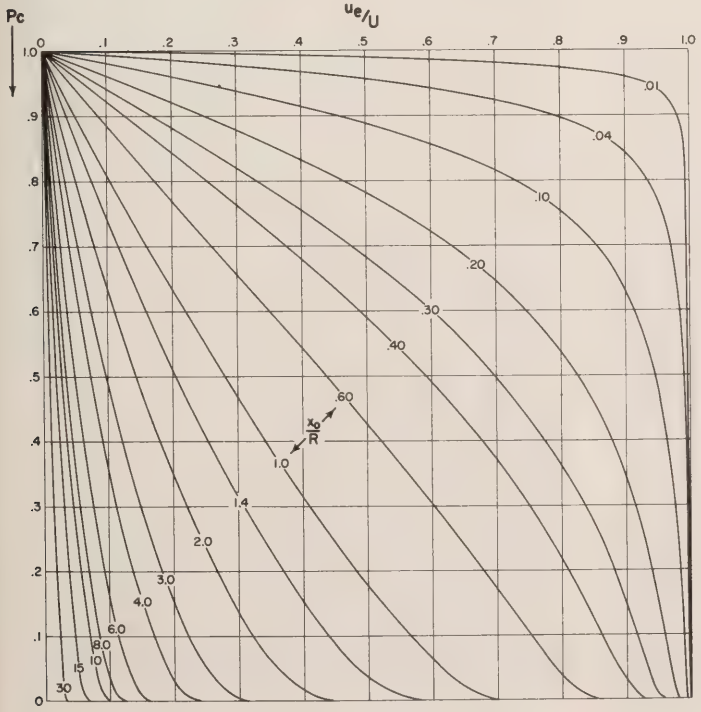


FIGURE 3.—Minimum probability of capture (P_c, ordinate) from equation (5), as a function of relative escape velocity, u_e/U, for various values of relative reaction distance, x_0/R. See Figure 1 for definition of symbols. Upper panel: Semilog graph to be used in analysis, where graphical calculations are required. Lower panel: Linear graph illustrating the behavior of the theoretical solution for all values of u_e/U.

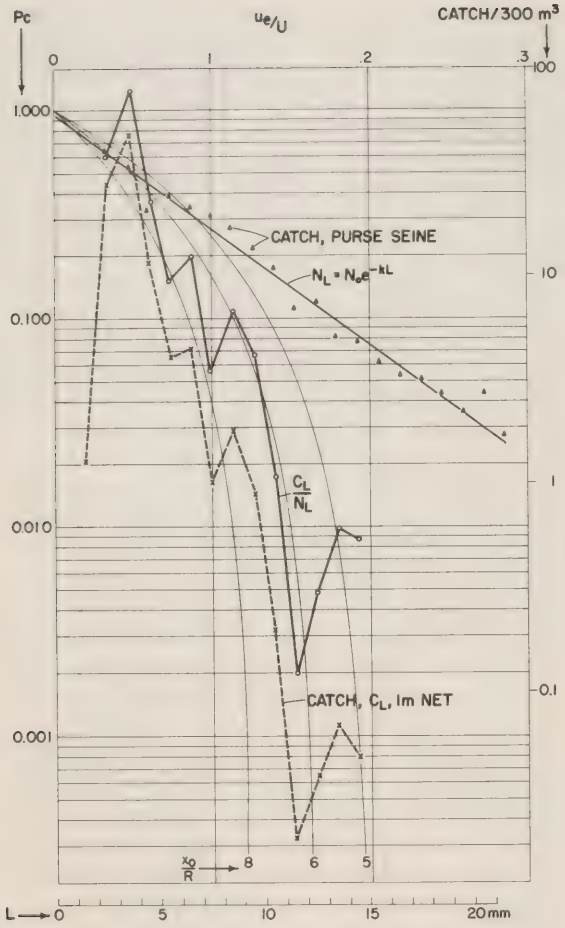


FIGURE 4.—Analysis of length-frequency data for daylight catches of *Stolephorus* from 44 paired samples. Purse seine data (triangles), a measure of absolute abundance, are approximated by the straight line, N_L. Catch with the 1-m net, C_L, has been corrected for changes in population (N) with length (L), to obtain the middle curve, C_L/N_L, which shows the minimum probability of capture, P_c, as a function of length for the 1-m net. Three theoretical curves for P_c at constant relative reaction distance (x_0/R) are reproduced from Figure 3, to show degree of fit between data and theory. Data from Murphy and Clutter (1972).

converted data can now be directly compared with the theoretical curves of Figure 3, three of which are shown on Figure 4 (the curves for P_c at $x_0/R = 5$, 6, and 8).

The adjusted 1-m net catch data fall near the theoretical curves for P_c at relative reaction distances, x_0/R, of 6 and 8; since $R = 0.5$ m for this net, the reaction distance of *Stolephorus* apparently ranges between 3 and 4 m. Murphy and Clutter (1972) obtain comparable results from an equation they derive for calculating x_0 directly. They used similar assumptions—in particular, an escape speed of $10L$ per second—but set $P_c = 1.0$ for the third class interval (3.5 mm). Here P_c was set at 1.0 at the intercept of the purse-seine catch curve with the ordinate axis, i.e., $P_c = 1.0$ at N_0, the fictitious population density at zero length, because only at this length does the assumed relationship between speed and length yield zero velocity. Since N_L, the population density at any given length L, is equal to N_0 for the adjusted data, the above procedure is internally consistent.

There are two exceptions to the otherwise fairly good fit between the adjusted data and the theoretical curves. The first, catch with P_c exceeding 1.0 for the third class interval (3.5 mm), may be due to sampling variability, overestimates of the water sampled by the purse seine, or underestimates of the water sampled by the 1-m net. It could also be due to less than optimum avoidance behavior by these small fish. The second exception, unexpectedly large catches in the three largest class intervals (12.5-14.5 mm) could be due to variability, or to a decrease in mean reaction distance for these animals, from a "normal" value of 3-4 m down to about 2.5 m ($x_0/R = 5$). Isaacs (1965) suggested that daytime tows should catch more than proportionate numbers of the sick, lame, or lazy; this effect should be most pronounced for the largest animals, which normally are the ones best able to dodge the net.

Minor fluctuations in the fit of the adjusted 1-m net data on Figure 4 are probably due to sampling variability, but to illustrate use of avoidance theory, suppose that the minor peaks and valleys for fish of intermediate sizes were significant. Note that these points tend to fall into two groups: those near the curve for P_c at $x_0/R = 6$, and others, $x_0/R = 8$. This could be an artifact due to schooling behavior, since group reaction should reduce the probability of capture below the theoretical minimum value for individual reaction. One measure of this effect

is an increase in the apparent reaction distance. Instead of the true value, x_0, we would expect to obtain an apparent value which approaches (x_0 + radius of the school) for large schools. If *Stolephorus* schools at all sizes represented on Figure 4, the different values of x_0/R, 6 versus 8, may reflect the presence of smaller and larger schools, differing in radius by about $2R$ or 1 m.

Some support for this apparently fanciful argument can be found in the *Stolephorus* catches obtained at night by Murphy and Clutter (1972). Night purse-seine catches showed marked peaks in abundance of fish in the 7-8 mm and 11-12 mm size classes and relatively low abundances in the 4- , 9- , and 14-mm class intervals. Simultaneous tows with the 1-m net, on the other hand, yielded precisely opposite results. The 1-m net apparently undersampled abundant size classes and was more effective with the less abundant size classes. This is precisely what is expected if the purse seine catches schools of various sizes equally well, whereas the 1-m net underestimates the abundance of schooled fish, more or less in proportion to school diameter, provided only that the fish school by size and that changes in abundance are associated with changes in school size, rather than changes in the number of schools.

This detailed treatment of a single set of length-frequency data is intended only as a demonstration of the amount of information which can be extracted from such observations in the light of theory, when and if measurements of typical reaction distances and escape velocities have been made. Results of this as-yet-tentative analysis may be summarized by saying that *Stolephorus* in the 1-m net sample apparently consist of:

A. Animals in the 1.5- and 2.5-mm class intervals, which are partially lost through the meshes and probably are unable to avoid the net.

B. Animals 3.5 mm long, which seem to be adequately retained by the meshes and apparently are too small to effectively avoid the net.

C. Animals 4.5 to 11.5 mm long, which react at about 3-4 m distance (proportionately more, or less, if their swimming speed is less, or more, than 10 body lengths per second). Maximum P_c for this group is about 0.35 for the 4.5 mm fish, dropping to 0.002 for the 11.5 mm fish.

D. Animals 12.5 to 14.5 mm long, which have anomalously large values of P_c when compared to group C, above. If these differences are significant, this implies that their reaction distances or swimming speeds, or both, may be abnormally low.

In the following examples there are no measurements of absolute abundance to compare with towed-net catch data, so assumptions will have to be made as to the relative contributions of population structure and avoidance to the outcome of sampling. Before making such assumptions it will be useful to consider the relative effects of these two factors in the case of *Stolephorus*.

On Figure 4 it can be seen that population abundance of *Stolephorus*, N_L, changed by a factor of 10 over the length interval sampled by the 1-m net. Over this same size interval the catch per class interval (C_L) changed by a factor of 1,000 or more. Thus N_L accounts for no more than 1% or 2% of the observed changes in catch length frequency, the remaining 98% to 99% being attributable to avoidance, at least for animals large enough to be fully retained by the mesh. In this strictly relative sense a 10-fold change in population density with size is in fact negligible, however important it may be in another context.

The problem of relative significance can be placed in perspective by considering whether data such as the 1-m net *Stolephorus* catches might be used to estimate population structure. Daylight 1-m net catches appear to be so overwhelmingly influenced by avoidance that even a 100-fold change in N_L might not be measurable since it could be obscured by a mere 10% error in estimating the effects of avoidance. In this sense it would be fair to assume that a population's structure is uniform, constant for all class intervals sampled by a given net if changes in N_L could not have been measured by that net. This can reasonably be taken to be true whenever the right-hand slope of the catch curves (C_L) exceeds the slope of the population curve

(N_L) by a factor of 10 or more, as it does in Figure 4.

When this assumption is made, however, it must be recognized that the results of any subsequent analysis are contaminated by whatever population structure effects are present and erroneously attributed to avoidance.

Anchovy (*Engraulis mordax*) larvae were also collected off southern California by Murphy and Clutter (1972) with a 1-m net and an Isaacs-Kidd midwater trawl (IKMT). Both nets had similar mesh size and were towed in daylight and at night at comparable speeds, nominally 75 cm/sec (although the IKMT may have been towed somewhat faster). Figure 5 shows data from these tows, converted to speed frequency by assuming that $u_e = 10L$. No estimates of absolute abundance were made for anchovy by Murphy and Clutter; the plankton purse seine was not used in these trials. However, Figure 4 shows that even 10-fold changes in N_L, abundance as a function of length, do not materially alter the shape of the *Stolephorus* speed-frequency curve. Essentially identical results could have been obtained by fitting the catch data to the theoretical curves without correction for changes in population density. Since anchovy are in many ways similar to *Stolephorus*, it may be tentatively assumed that avoidance is the major determinant of size-frequency curves for anchovy, as it clearly was for *Stolephorus* (Figure 4).

Without an independent estimate of absolute abundance, there is no priori relationship between catch and P_c. This relationship must therefore be established by seeking the best possible fit between theory and observations. Speed-frequency values were plotted on tracing paper, using the semilog coordinate system of Figure 3. The resulting graph was placed over the upper panel of Figure 3 and moved up and down until a good fit resulted (right-left motion is not allowed, since the position of points along this axis is determined by size, the size-speed relationship, and net speed). This procedure is equivalent to making various assumptions about N_0, the fictitious population density at zero length, for which $P_c = 1$ by definition since $u_e = 0$. When this is done, the speed-frequency curves become speed - P_c curves, showing probability of capture for each class interval. Best fits were obtained for the 1-m net anchovy catches with $N_0 = 75$ anchovy per 100 ml wet plankton (left panel, Figure 5). For the IKMT, the best fit yielded $N_0 = 60$ anchovy per 100 ml wet plankton (right panel, Figure 5). It might have been worthwhile to treat day and night catches separately, as was done for the two types of gear, but the resulting differences in N_0 between day and night tows are small, change sign for the two different nets, and probably are not significant.

Figure 5 shows that the variance for anchovy data was smaller than that for *Stolephorus* catches (Figure 4), so that the anchovy data fit the theoretical curves somewhat better. There is no way to tell whether this difference in variance is due to differences in sampling or population structure. For both nets, day-night differences in x_0/R are small, but reaction distances tend to be slightly greater for tows taken during the day, as might be expected. A surprising result is the similarity in values of x_0/R obtained for the two nets: about 6.6 for the 1-m net and 5.4 for the IKMT (if slightly lower values for the largest size classes are ignored). This yields reaction distances, x_0, of 3.3 m for the 1-m net and 8.2 m for the IKMT. Clearly anchovy reacted to the IKMT at considerably greater distances. A light dashed line on Figure 5 (right panel) shows the dramatically increased catches which would be expected if anchovy had reacted to the IKMT at 3.3 m ($x_0/R \simeq 2$), as they apparently did in the case of the 1-m net.

The analysis shows that maximum values of P_c for the IKMT amounted to only 0.25, as compared to maximum values of P_c for the 1-m net of 0.40 or more.

Mesh retention appeared to differ for the two nets, despite similarity in mesh size (according to Murphy and Clutter, 1972, the IKMT was meshed with Nitex,[3] and the 1-m net with gauze silk, 56xxx grit, having openings of 0.505 and 0.55 mm, respectively). Retention dropped below 100%, based on deviations from the the-

[3] Reference to commercial products does not imply endorsement by the National Marine Fisheries Service.

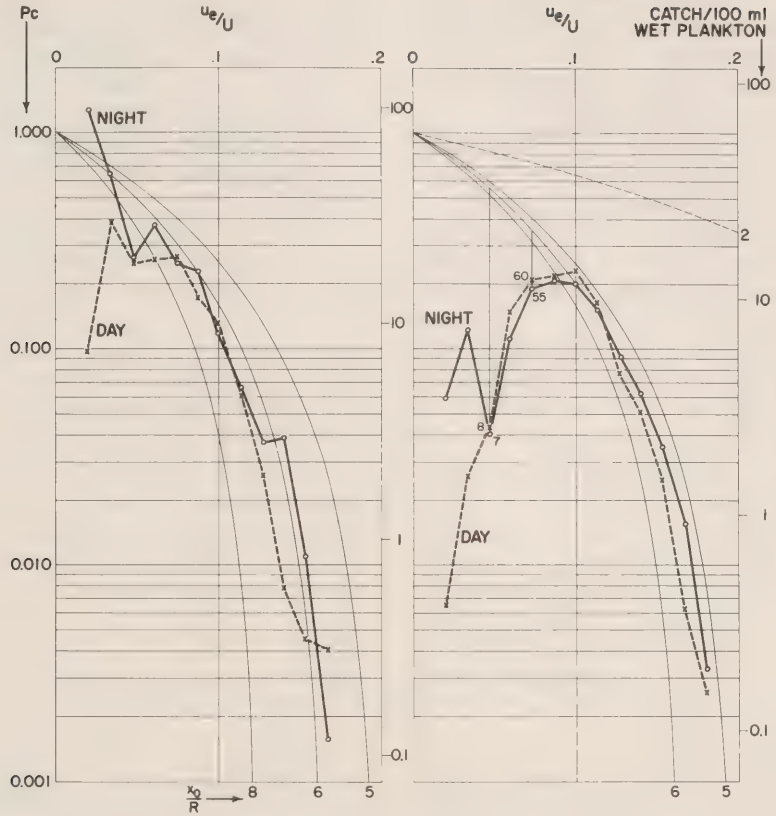


FIGURE 5.—Day and night catches of larval anchovy by a 1-m net (left) and an Isaacs-Kidd midwater trawl (right). Length-frequency data have been converted to relative escape speed (abscissa) versus frequency (ordinate, right hand scales), and compared with theoretical curves. Catch values at $P_c = 1.0$ provide estimates of abundance for all class intervals sampled. Dashed line for P_c at $x_0/R = 2$ on Isaacs-Kidd graph shows catches which could have been expected if the anchovy's reaction distance had been equal to that for the 1-m net. Net retention, based on differences between theoretical and actual catch, is shown for two class intervals on right panel: 7% to 8% for 3.75 mm fish and 55% to 60% for 5.75 mm fish. (Class sizes ranged from 1.75 mm to 12.75 and 13.75 mm by 1 mm increments.) Data from Murphy and Clutter (1972).

oretical lines of constant x_0/R, for anchovy shorter than 7.75 mm with the IKMT and 4.75 or 5.75 mm for the 1-m net. If x_0/R for a given species remains constant for any one net towed at a single speed, extrapolation of the theoretical curve toward the origin gives an indication of expected catch for smaller size classes (assuming, of course, that changes in population density with length are negligible). This use of avoidance theory is illustrated in Figure 5, right panel, where retention is calculated at 7% to 8% for 3.75-mm fish and 55% to 60% for 5.75-mm fish. These values can be easily measured on the semilog graph; the vertical distance between the "theoretical" and the observed values is transferred to the vertical coordinate scale (e.g.,

with dividers), setting the upper point at 1.0 (100%) and reading the fraction or percentage retained at the lower point.

Let us now consider catches obtained with one type of gear at two different speeds.

Aron and Collard (1969) made carefully controlled IKMT tows at two different speed ranges, at night, using telemetering flow and depth meters to insure that the amount of water sampled was the same for all tows and that sampling was done at the desired depths. The speed of their net varied between about 1.0 and 1.7 m/sec and about 1.6 and 2.3 m/sec during the two sets of tows; I have assigned values, corresponding to modal speeds, of 1.2 and 2.0 m/sec to these tows for calculating values of u_e/U.

The assumption made thus far that $u_e = 10L$, cannot be used for the species enumerated by Aron and Collard because of their large size (up to 102 mm); escape speeds of 10 body lengths per second yield values in excess of the net's speed. Either fish that big should not have been captured, or their escape speed must be considerably less than 10 lengths per second. Accordingly, it was assumed that $u_e = 5L$ (with units of cm/sec and cm).

As was noted earlier, the effect of different choices of escape velocity to length ratios is to shift the observed points along the u_e/U axis of Figure 3, with proportional changes in resulting values of x_0/R. If a set of observed points fall precisely on the theoretical curve $x_0/R = 4$, for example, a twofold change in the assumed escape velocity results in points falling equally precisely on the curves for $x_0/R = 8$ or 2, depending on whether the escape velocities are halved or doubled. Values of P_c are not affected by the choice of velocity to length ratios.

Obviously, relative values of reaction distance, x_0, can be estimated from the present theory, but absolute values can only be determined if in addition the animal's actual escape velocities are known, preferably as a function of size. Thus, from Figure 5 we can conclude with some assurance that anchovy react to the IKMT at distances some 2.5 times as great as they do to the 1-m net. But the reaction distances themselves, 8.3 m for the IKMT and 3.3 m for the 1-m net, can only be correct if anchovy do in fact swim at an average speed of 10 body lengths per second when trying to avoid the net.

Of the species enumerated by Aron and Collard, *Bathylagus stilbius* seemed most amenable to analysis with avoidance theory, because the length-frequency curves for this species were somewhat smoother, and differed more with speed of tow, than was the case for other species. Figure 6 shows the speed-frequency curves for this species, assuming that $u_e = 5L$ and that $U = 120$ and 200 cm/sec, respectively. A fairly good fit could be obtained for P_c at $x_0/R \simeq 3.8$ for the faster tow and for part of the slower tow. For the fit shown in Figure 6, N_0, the abundance at zero length, is 1,400 animals per class interval (Aron and Collard, 1969, give catches as total numbers caught during all 34 tows made in January 1966). An alternative choice of N_0, 340 animals per class interval, produces a good fit with $x_0/R = 2.4$ for the larger animals caught by the slower tows but does not fit any of the other data. In short, there is no way to fit the length-frequency data for *B. stilbius* to the theory under the assumptions used up to now.

The assumption most likely to be violated is that population size at different lengths has negligible influence on the size-frequency curve ($N_L \simeq N_0$). This assumption when valid makes it possible to fit data from a series of length classes using a single value for N_0, as was done for anchovy (Figure 5). If N_L varied significantly with length for *B. stilbius*, only identical length classes can be compared between the two sets of tows at different speeds. Figure 7 illustrates this procedure for the 62- and 97-mm length classes, where theoretical curves for P_c at $x_0/R = 2.8$ and 1.8, respectively, fit the data for these two size classes. Values of N_0 thus obtained were 900 individuals per class interval for 62-mm fish and 26 individuals per class interval for 97-mm fish. This 35-fold difference in apparent abundance is comparable in magnitude to differences in catch rates, 285 to 8 (48-fold) for the faster tows and 57 to 1 for the slower tows. It therefore seems likely that the shape of the length-frequency curves for *B. stilbius* was determined in large part by the population structure; avoidance apparently played

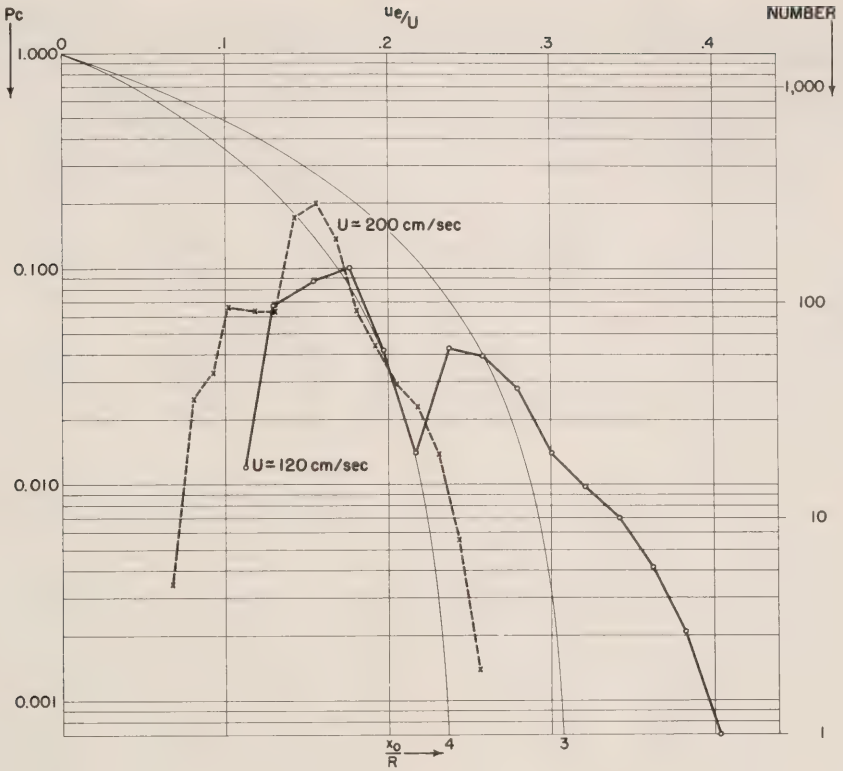


FIGURE 6.—Catches of *Bathylagus stilbius* with an Isaacs-Kidd midwater trawl at two speeds. Length frequencies converted to speed frequencies are compared with theoretical curves for P_c, showing fairly good fit at $x_0/R \simeq 3.8$ for part of data. No overall fit is possible for these observations, indicating that length-frequency curves for this species were not determined primarily by avoidance. Data from Aron and Collard (1969).

a minor role, accounting only for the difference between the 35-fold range in apparent abundance and the observed 48- to 57-fold differences in catch rates for the 62- and 97-mm size classes. The most important effect of avoidance in the *B. stilbius* catch data is the nearly constant 5-fold difference in catch rates at the two different speeds, for all animals larger than 62 mm.

Figure 7 shows sample results for only two class intervals. Table 1 shows results for all class intervals of Aron and Collard's *B. stilbius* catch data: Catches (as read from length-frequency curves), ratios of catches at two speeds, and values of x_0/R, N_0, and P_c obtained by fitting the catch data to the theoretical curves of Figure 3. Obviously, "fitting" two points to a curve is a trivial exercise, which is only justified by the apparently consistent results obtained for larger fish in Table 1. Data from three or more sets of tows, at as many different speeds, should be used for such analyses.

Figure 7 also shows the ranges of values of u_e/U, and the extreme values for x_0/R and N_0, which result when the full range of net speeds reported by Aron and Collard (1969) is used instead of the modal speeds. The numerical results, like the net speeds, vary by factors of about two—an indication of the uncertainty inherent not only in the *B. stilbius* data but also in the data for other species considered here, since variations in net speed comparable to those measured by Aron and Collard are doubtless present

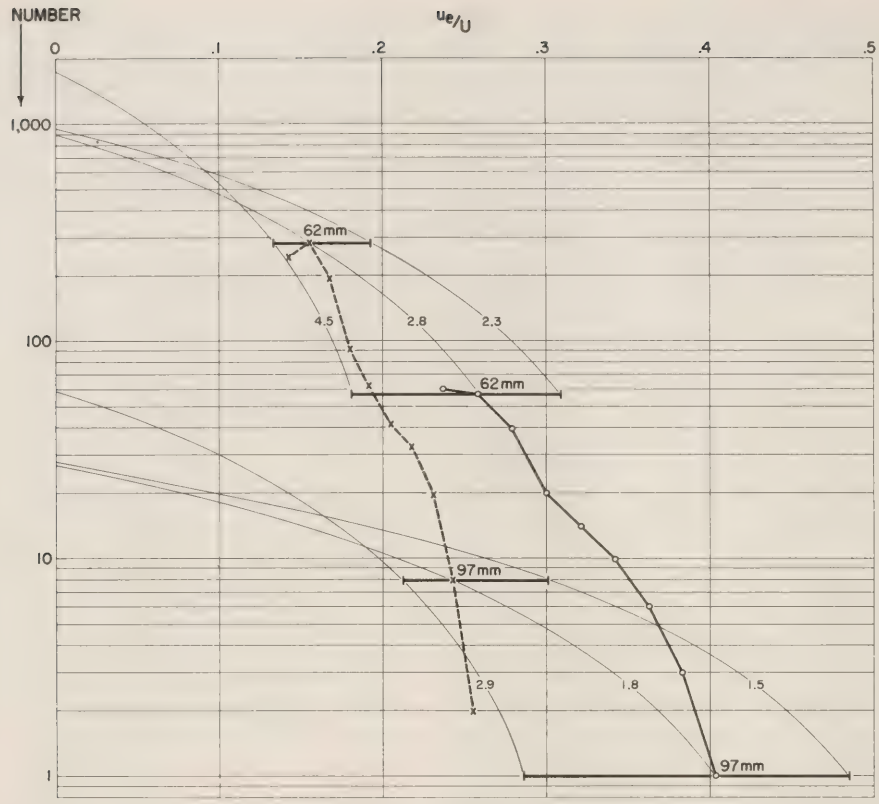


FIGURE 7.—Alternative analysis of *Bathylagus stilbius* data from Figure 6. Estimates of population (intercept of x_0/R curves for 1.8 and 2.8 with ordinate) by class interval show wide variations: from 900 animals at 62 mm to 26 animals at 97 mm. This range is comparable to the observed range in catch for these class intervals (57 to 1), showing that the length-frequency curves are primarily determined by population structure. Horizontal bars show measured ranges of towing speeds, and the effect of different speeds on the analysis. Data from Aron and Collard (1969).

during any normal towing procedure. This uncertainty does not affect the qualitative conclusions obtained from theoretical analyses; it is quite clear, for example, that anchovy react earlier to the IKMT than they do to the 1-m net. It is also quite clear that the population structure of *B. stilbius* determines the shape of the catch size-frequency curve, whereas differences in overall levels of catch for this species at two ranges of towing speed are due to avoidance, at least for those animals effectively retained by the meshes. In any case, numerical estimates of parameters such as P_c and population density which are correct to within a factor of two or less are entirely adequate for many purposes.

Simultaneous solutions for P_c as a function of length have been obtained from the theoretical equations for three pairs of samples from as many populations. The results, while not definitive, appear encouraging.

It should therefore be possible to apply the theory to a more typical set of data, a single composite sample of larval and juvenile stages of *Katsuwonus pelamis*, the skipjack tuna. These animals were sampled with a large midwater trawl, the Cobb pelagic trawl (Higgins, 1970), during a series of five equatorial cruises made by the RV *Townsend Cromwell* in 1969-70. Repli-

TABLE 1.—Analysis of catches of *Bathylagus stilbius* with an Isaacs-Kidd midwater trawl towed at two speeds, based on avoidance theory as illustrated in Figure 7. Data from Aron and Collard (1969).

Standard length (mm)	Catches		Catch ratio	Relative reaction distance x_0/R	Population abundance number per class interval	Probability of capture		Notes
	Low speed	High speed	High speed / Low speed			Low speed	High speed	
27	17	5	0.29	--	--	--	--	[1]
32	93	36	0.39	--	--	--	--	[1]
37	127	46	0.36	--	--	--	--	[1]
42	143	94	0.65	--	--	--	--	[1]
47	60	90	1.5	1.8	150	0.41	0.61	[2]
52	20	90	4.5	3.3	300	0.068	0.31	[2]
57	61	248	4.1	2.9	720	0.085	0.34	[2]
62	57	285	5.0	2.8	900	0.063	0.31	--
67	40	195	4.9	2.6	660	0.061	0.31	--
72	20	92	4.6	2.3	280	0.073	0.33	--
77	14	63	4.5	2.1	200	0.071	0.32	--
82	10	42	4.2	1.9	120	0.084	0.25	--
87	6	33	5.5	1.9	100	0.060	0.33	[3]
92	3	20	6.7	1.9	62	0.050	0.33	[3]
97	1	8	8.0	1.8	26	0.036	0.29	[3]
102	0	2	--	--	--	--	--	--

[1] Mesh losses probably significant, analysis with avoidance theory inappropriate.
[2] Mesh losses may be significant, analysis with avoidance theory questionable.
[3] Sample size inadequate, results of analysis may be seriously in error.

cate 6-hr tows were taken every night for (usually) five successive nights at each of five locations (lat 12°N, 7.5°N, 3.5°N, 0°, and 3.5°S at long 145°W) during these cruises. Catches of skipjack larvae and juveniles during each of these cruises are summarized in Table 2.

Length-frequency data from three cruises, numbers 43, 44, and 48, were kindly made available to me by Walter M. Matsumoto. These data were similar for all three cruises and were therefore pooled to obtain a smoother curve (Figure 8, right panel). Of the 510 animals in this sample, 6 could not be measured. Another 5, the largest (see Figure 8, right panel) were suspected of being atypical, possibly moribund and unable to properly avoid the trawl. Figure 8 (left panel) shows the data for the remaining animals, converted to speed frequency using $u_e = 10L$ and $U = 150$ cm/sec.

Since the skipjack population structure as a function of length, N_L, is completely unknown, two extreme assumptions are considered: First, that avoidance has no effect, so that virtually all of the drop in catch with increasing length (Figure 8) is due to changes in the population. Second, that population structure has no effect, so that the length-frequency curve is determined only by avoidance and mesh losses.

The first assumption is illustrated in Figure 9, left panel, where the lowest curve shows speed-frequency values. The straight line represents N_L, assuming the largest possible exponential decrease in population with size, consistent with the catch data. The upper curve shows P_c, obtained by dividing the catch data by N_L after setting $N_0 = 1.0$, exactly as was done on Figure 4. This analysis results in a wide range of values for P_c and x_0/R. N_0 in this case becomes 100%, equivalent to 500 individuals per class interval. Figure 9, right panel, shows P_c plotted on the linear theoretical graph of Figure 3.

The alternative extreme, assuming that $N_L = N_0$ so that population has no influence on catch length frequencies, is illustrated in Figure 10. There is no single apparent "best fit," between observation and theory, so three alternatives are considered. The upper curves, marked A, show

TABLE 2.—Skipjack larvae and juveniles caught with the Cobb pelagic trawl during RV *Townsend Cromwell* equatorial cruise series. Samples were taken along long 145°W, at lat 12°N, 7.5°N, 3.5°N, 0°, and 3.5°S.

Cruise no.	Dates	Number of tows	Number of successful tows	Skipjack caught
43	May 7-June 2, 1969	24	16	197
44	July 6-Aug. 3, 1969	25	10	154
46	Oct. 14-Nov. 13, 1969	27	11	297
47	Jan. 20-Feb. 25, 1970	21	1	1
48	Mar. 30-Apr. 30, 1970	25	15	158

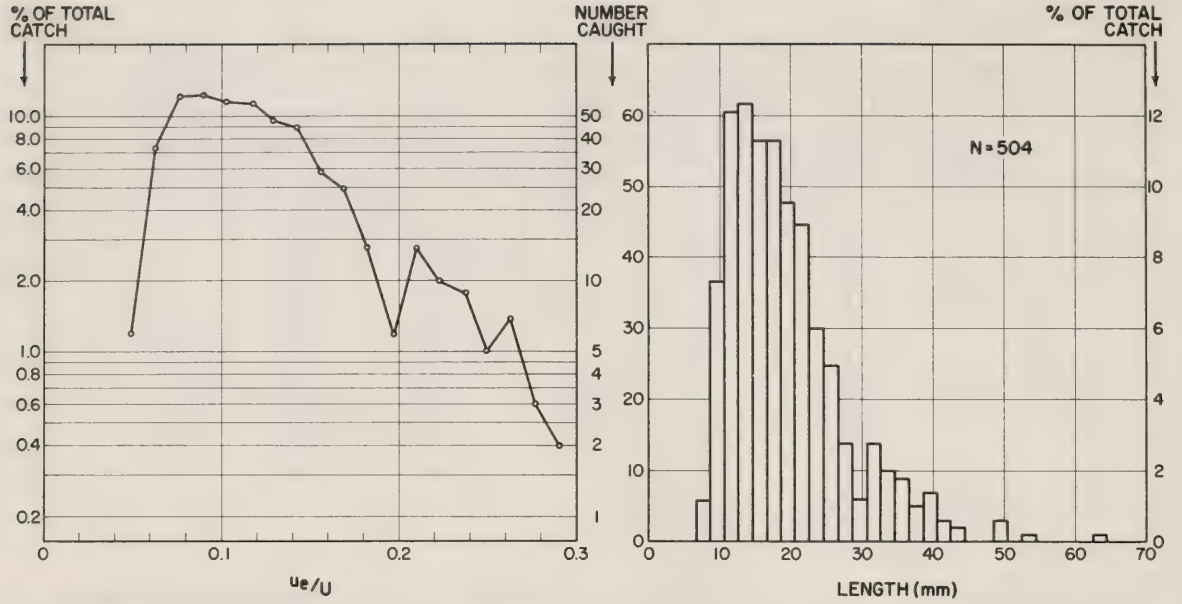


FIGURE 8.—Speed-frequency curve for skipjack larvae caught by a Cobb pelagic trawl (left panel) obtained from a length-frequency curve (right panel). Data courtesy of W. M. Matsumoto, NMFS, Southwest Fisheries Center, Honolulu Laboratory.

the data aligned to yield a fit for the best sampled class intervals. The lower curve, C, is aligned so as to fit the theoretical curves in regions of maximum slope, where sampling is most sensitive to avoidance. The middle curve, B, is a compromise which yields a reasonable fit at intermediate class intervals. Although all three analyses look plausible in the left panel of Figure 10, the linear graph shown on the right of Figure 10 clearly demonstrates that curve B yields the best match between theory and observation.

In principle there is no reason to prefer the analyses shown on Figure 10 to their alternative, Figure 9. However, I personally regard curve B on Figure 10 as the best solution because it provides the simplest and most informative explanation for the observations.

Note that all three sets of curves on Figure 10 fit two separate theoretical curves, in two distinct and well-separated groups of class intervals. As in previous examples, P_c for the largest animals markedly exceeds the values which would be expected if the theoretical x_0/R curve for smaller animals were simply extrapolated toward the right (except for curve A). In the cases of *Stolephorus* and anchovy, these anomalies were relatively minor and could reasonably be attributed to selective sampling of animals with subnormal avoidance ability. In the case of skipjack, however, this anomaly is more pronounced.

A more likely explanation for the two-part curves of Figure 10 is the construction of the Cobb trawl, which is lined with netting of two different mesh sizes: 19 mm stretched mesh of 9-thread (210 denier) nylon netting in the forward sections, with 6.4 mm stretched mesh 6-thread (210 denier) nylon netting at the cod end (Higgins, 1970). This 3-fold difference in mesh size corresponds with a nearly 3-fold difference in the size of skipjack which makes up the two components of the catch (100% apparent mesh retention at lengths greater than 15.5 mm and 37.5 mm, respectively, from curve B of Figure 10). The Cobb trawl is, in effect, two distinct nets which happen to be rigged in tandem. The openings of the trawl and its cod end during a tow are estimated to have radii of about 4 m and 1.5 m, respectively, so that their mouth areas differ by a factor of seven. The volume of water filtered by the cod end should thus

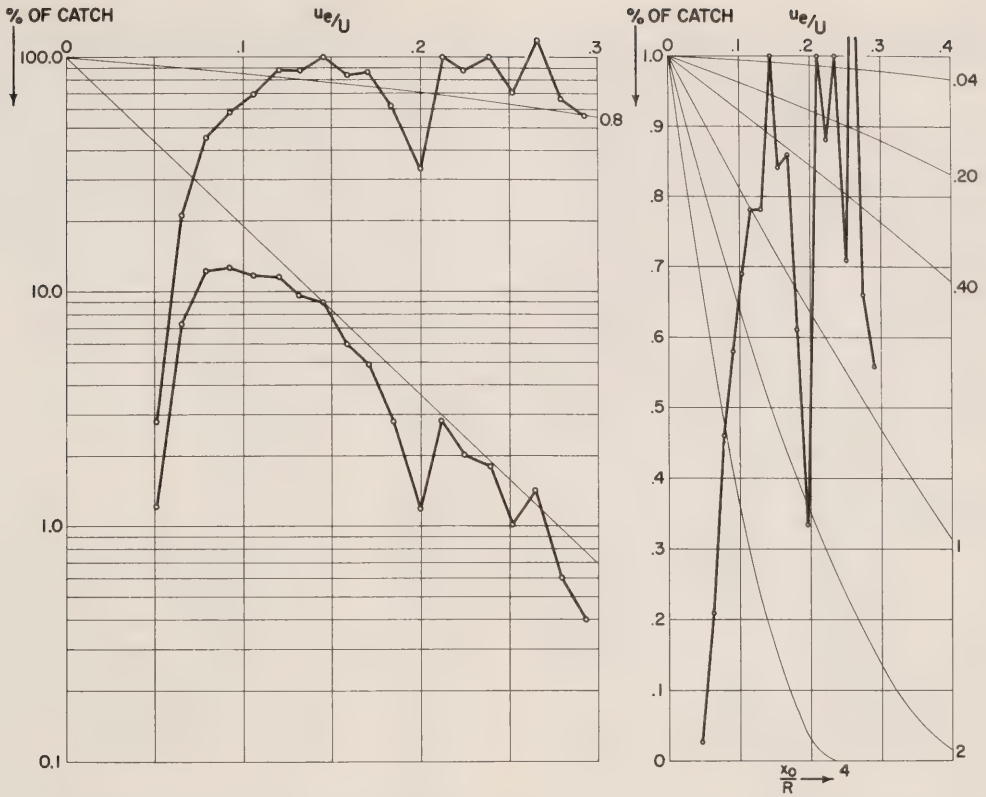


FIGURE 9.—One possible analysis of skipjack catch data, Figure 8, assuming that the length-frequency curve is determined by population density. Left panel: Lower curve, speed-frequency data, Figure 8. The straight line represents a hypothetical population density curve. Upper line shows P_c obtained by correcting catches for population changes. Right panel: Values of P_c from left panel, plotted on linear coordinates.

be somewhat less than one-seventh of the volume sampled by the trawl, because of the increased resistance to flow of the finer mesh. Catches of the six largest class intervals of skipjack all exceed the "expected" catch (theoretical curve for $x_0/R = 4$) by factors of seven or more, as would be expected if in fact these larger fish were captured by the main body of the trawl, rather than by the cod end.

The evidence suggests that curve B on Figure 10 represents a reasonable analysis of skipjack catches with the Cobb trawl. This implies that avoidance and mesh losses are dominant factors determining the size-frequency curves (Figure 8). The largest skipjack, 31.5 to 43.5 mm in length, were captured by the main body of the Cobb trawl, with P_c values between 0.05 and 0.009. Their reaction distance, x_0, was $3R$, or some 12 m. Some losses through the coarse mesh are apparent for animals smaller than 39.5 mm in length. Skipjack smaller than 31.5 mm in length were captured by the cod end of the trawl, at P_c values ranging from about 0.3 to 0.03, corresponding to reaction distances of $4R$, or 6 m. Some losses through the finer mesh are apparent for animals smaller than 17.5 mm; estimated mesh losses reach 96% for animals 7.5 mm in length. As was pointed out earlier, the above estimates of reaction distances are dependent on the assumed escape speeds, 10 body lengths per second. If the animals move faster than this, x_0 values will diminish proportionately, and vice versa.

Estimates of Pc are not affected by escape

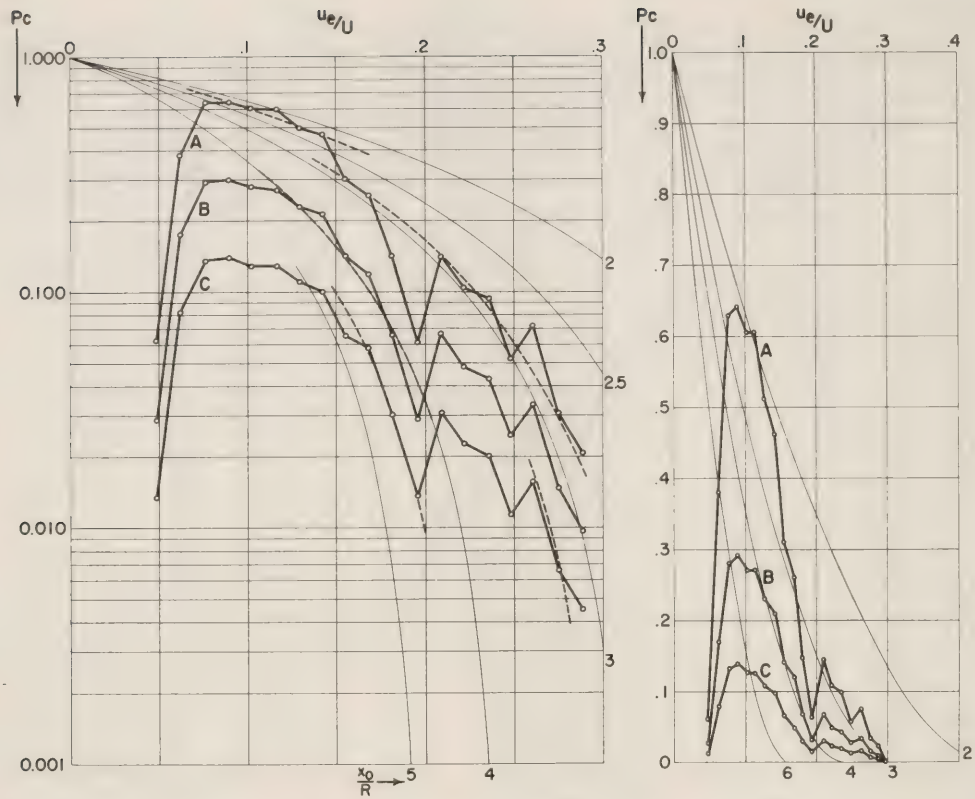


FIGURE 10.—Alternative analysis of skipjack data from Figure 8, assuming constant population density. Left panel: Three possible choices of fit between catch data and theoretical curves of P_c at constant x_0/R. Curve A shows fit for best sampled class intervals. Curve B shows fit for midrange class intervals. Curve C shows fit for regions of maximum slope. Right panel: P_c curves from left panel, plotted on linear coordinates.

speed assumptions, so the analysis yields usable estimates of population abundance of skipjack larvae and juveniles between 17.5 and 43.5 mm in length, if population structure is not important. From curve B of Figure 10, N_0 is 40% (of 499) or 200 individuals per class interval, as can be seen by placing the "% of catch" scale of Figure 9 in the proper position on Figure 10. Since abundance apparently does not seriously affect the length-frequency curve, each of the 19 class intervals sampled must also represent a population of about 200 individuals. Thus the sample of 510 skipjack was taken from a population of about 3,800, an overall catch efficiency of 13%. The total catch resulted from 41 effective tows (out of 74), an average catch per effective tow of 12.3. Accordingly, the population sampled by the Cobb trawl must have numbered roughly 94 skipjack per effective tow, to yield the observed catches at 13% efficiency. By far the greatest number of skipjack were caught by the cod end of the trawl, so the volume effectively sampled was not more than 230,000 m^3 (100% filtering efficiency). This leads to an estimated mean population density for larval and juvenile skipjack of one fish per 2,500 m^3, in areas where skipjack were present during the three *Townsend Cromwell* equatorial cruises.

Since P_c is by definition a minimum probability of capture, reference to equation (3) shows that the above estimate of mean population density (during a tow) represents a maximum value. On the other hand, of course, the skipjack probably were not randomly distributed, so that

a 6-hr tow doubtless underestimates their actual (as opposed to mean) population density by integrating over a 33-km distance.

Finally, two of the four species discussed here were sampled in a manner which permits use of equation (8) to estimate values of K (the product x_0u_e). Anchovy were sampled with two different nets at one speed of tow, and *B. stilbius* were sampled with one net at two ranges of speed. Table 3 shows values of K calculated for these two species. For any one choice of speeds, values of K for *B. stilbius* are nearly constant within the class intervals where fish were retained by the mesh and caught in numbers large enough to yield useful estimates of C_1/C_2, the ratio of catches obtained at the two speeds. Values of K for anchovy, on the other hand, were not constant. The latter result is not surprising, since widely different values of x_0 were obtained for the 1-m net and the IKMT whereas u_e would not be expected to differ for the two nets. Accordingly, the product of x_0u_e should not be the same for both nets, which violates the basic assumption used in calculating K with equation (8).

When values of K from Table 3 are used to calculate P_c from equation (7), the results agree with those obtained graphically for *B. stilbius* at the modal speeds, but not for anchovy. Apparently the calculated values of K for anchovy in Table 3 are too low, since they yield values of P_c which are too high, corresponding to values expected for reaction distances of about 2 to 3 m for both nets. Until avoidance behavior is better understood, equation (8) should be used with caution.

SUMMARY AND CONCLUSIONS

The ideal sampler for plankton and nekton is one whose selective characteristics are known to be appropriate, qualitatively and quantitatively, for the problem under study. Major factors determining the selectivity of towed-net samplers are avoidance and mesh selection, both of which are strongly dependent on species, size or stage of development, and physical condition. Thus the theory of towed-net selectivity must be based on a combination of general principles and detailed knowledge of the physical characteristics and behavior of each species of interest, and of each net design as well.

This preliminary study deals with one aspect of selectivity: the basic principles of avoidance. A theoretical equation is derived for P_c, the minimum probability of capture, for animals which respond individually to an oncoming sampler by attempting to dodge. The theory is based on the amount of time animals allow themselves for avoiding the net, the animal's speed relative to the net, and the geometry of the encounter. Animals are characterized by their reaction distance, x_0, and their escape speed, u_e. The net is characterized by the radius of its mouth opening, R, and its speed through the water, U. Equations (5) and (6) show the theoretical relationships between these variables and P_c; Figure 3 illustrates these equations graphically.

TABLE 3.—Values of the product $x_0u_e = K$ for anchovy and *Bathylagus stilbius*, from equation (8). Anchovy data obtained with two nets towed at one speed, day and night. *B. stilbius* data obtained with one net towed at two speed ranges; K calculated using minimum, modal, and maximum speeds for each range.

Anchovy					*Bathylagus stilbius*				
Length (mm)	Catch ratios (1-m/IKMT)		K (cm²/sec)		Length (mm)	Catch ratios (slow/fast)	K (cm²/sec)		
	Day	Night	Day	Night			Minimum speeds	Modal speeds	Maximum speeds
7.75	0.735	0.764	758	665	47	0.667	5,600	6,500	11,800
8.75	0.492	0.565	1,470	1,240	52	0.222	11,200	13,300	20,700
9.75	0.431	0.524	1,850	1,360	57	0.244	11,000	13,000	20,300
10.75	0.209	0.827	2,410	488	62	0.200	11,500	13,600	21,100
11.75	0.242	0.417	2,280	1,690	67	0.204	11,500	13,500	21,000
12.75	0.847	0.133	435	2,710	72	0.218	11,300	13,300	20,800
					77	0.222	11,200	13,300	20,700
					82	0.238	11,100	13,000	20,400
					87	0.182	11,700	13,900	21,400
					92	0.149	12,100	14,400	21,900

Testing of the theory requires some knowledge of a species' escape speed as a function of size or stage of development and its reaction distance for one or more net designs under various circumstances, so that particular groups of animals in a sample can be associated with the proper values of x_0 and u_e in the theory. If the theory is known to be valid in a given instance, x_0 can be determined once u_e is known.

The theory was evaluated against four selected sets of catch data. Since not enough was known about the swimming ability of the species in question, assumptions had to be made about swimming speed as a function of size for each one. Aside from the major premise used in deriving the theory, that animals which can escape will do so, other assumptions made in carrying out analyses of catch data were: that reaction distance is essentially constant for any one species under a given set of circumstances (one net, towed at one speed, at one time of day) and that the size-frequency curve for a species is determined entirely by mesh losses, avoidance, and the population structure—the number of animals in each size class interval in the population.

The theory was first applied to daytime catches of *Stolephorus purpureus* with a 1-m net. Simultaneous measurements made with a plankton purse seine provided information on the population structure. This nearly ideal set of data permits direct calculation of the sampling efficiency of the 1-m net, so that an absolute test of the present theory could be made. First, the bias due to population structure was removed, by dividing the catch in each class interval by the population in that class interval; this procedure also converts the catch into values of P_c for fish large enough to be completely retained by the meshes, as equation (3) demonstrates. The adjusted catch curve (the solid line labeled C_L/N_L in Figure 4) can be directly compared with theoretical curves from Figure 3 (showing P_c for various values of relative reaction distance, x_0/R), when the length class intervals have been converted to speed class intervals by assuming that the fish swim 10 body lengths per second. Agreement between theory and observation appears to be good, with some exceptions. These may be due to sampling variance, population variance, or failure of one or more assumptions used in matching *S. purpureus* to the theoretical parameters. In the latter case, the anomalies could be accounted for by incompetent avoidance behavior and school response instead of individual reaction to the net.

In the second example, the theory was used to evaluate catches of anchovy by two different nets, a 1-m net and an IKMT, towed at the same nominal speeds. Since population abundance was not determined for anchovy, an additional assumption had to be made: that the catch length-frequency curves were determined primarily by avoidance and mesh losses, as in the case of Hawaiian anchovy, where catches decrease 1,000-fold while the population decreases only by a factor of 10 in the same size interval. With this assumption, catch speed-frequency curves must also be curves of relative P_c as a function of size, or speed. Fitting the observed values to the theoretical P_c curves (Figure 5) yields a unique value for population density in each class interval, numerically equal to the catch at $P_c = 1.0$. For the anchovy, population densities of 75 and 60 animals per 100 ml wet plankton were obtained for the two samples analyzed by this method. In this case agreement between theory and observation, and between samples, seems excellent. Except for night tows with the 1-m net, values of P_c do not exceed 0.40 for the 1-m net and 0.12 for the IKMT. The only significant deviations from theory occur at smaller class intervals, where mesh losses are important. Mesh retention can be estimated quantitatively by extrapolating the theoretical curve toward smaller class intervals, for comparison with observed catches, as illustrated on the right-hand panel of Figure 5.

The third example makes use of length-frequency data for *Bathylagus stilbius* caught with an IKMT towed at two different ranges of speed. In this case, no satisfactory fit could be achieved for all larger class sizes of both sets of tows, when treated as a unit. If instead the analysis is performed using only one class interval at a time from the two sets of tows, as shown in Figure 7 and Table 1, the cause of the difficulty becomes clear. The estimated population densities have almost as great a range as do the

catches. Therefore the length-frequency curves are primarily determined by population structure, not avoidance. However, avoidance does account for the fact that faster tows caught nearly five times as many fish. Table 1 shows that P_c remained essentially constant for each set of tows over a wide range of class intervals, with values of about 0.3 for the fast tows and 0.07 for the slower ones.

The final example illustrates the use of avoidance theory for analysis of a more typical set of catch data: larvae and juveniles of the skipjack tuna caught with one net towed at one speed. The simplest way to account for the skipjack data is to assume that avoidance was more important than population structure (Figure 10). The Cobb pelagic trawl used to sample skipjack had two sizes of mesh, differing by a factor of three; the smaller mesh was used to line the cod end of the Cobb trawl. Catches of skipjack with this net fall into two groups differing in size by a factor of about three, suggesting that this trawl acts as two nets fishing in tandem. The large mesh forward end catches the largest fish, with a maximum P_c of the order of 0.03. The cod end catches smaller fish, with maximum P_c values of about 0.3. Fish of intermediate size are able to dodge the cod end but some 10% to 50% of these fish (depending on size) were retained by the larger meshes.

Analysis of four test cases leads to the conclusion that the elementary avoidance theory developed here does in fact provide reasonable interpretations of some samples obtained with towed nets. The theory's major virtue is its ability to provide relatively unambiguous estimates of probability of capture and thus of animal abundance in nature, which are not dependent on the accuracy of assumptions about swimming speeds or reaction distances. Even when the theory fails to account for observed features of the catch, it provides useful insight into the reasons for such failure and some indication of their magnitude. This is most clearly evident for losses through the mesh, but failures of the theory, or of the assumptions used in applying it, are also responsible for evidence uncovered here of incompetent avoidance behavior by smaller animals, effects of schooling on avoidance success, and the fact that avoidance has only a minor effect on the length frequencies of *B. stilbius* samples. Given our present lack of knowledge of the behavior of animals when confronted by towed samplers, it might even be said that anyone using this theory should be most cautious in precisely those cases where the theory apparently works best. A case in point is the analysis of anchovy data presented on Figure 5. Agreement between observations and theory is relatively good in this case, so that it might be easy to forget that the slope of both curves, and the apparently valid estimates of reaction distance obtained from their slopes, depend entirely on the assumed relationship between the anchovy's length and its swimming speed. Similarly, Figure 7 shows the errors which can result from assuming that the speed of the net is constant. The best contribution to the study of plankton and nekton which the present theory could make is to stimulate further research which will make the theory obsolete.

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SWIMMING AND FEEDING BEHAVIOR OF LARVAL ANCHOVY *ENGRAULIS MORDAX*

JOHN R. HUNTER[1]

ABSTRACT

The swimming and feeding behavior of laboratory-reared larval anchovy, *Engraulis mordax*, was described over the first 30 days of larval life. Estimates were made of cruising speed, proportion of time spent in rest, and burst speeds. Tail beat frequency, tail beat amplitude, and speed of swimming larvae were measured from cine photographs and the relationship between these variables determined. Complete and incomplete feeding sequences were described in detail from cine photographs and the frequency of feeding acts determined from visual observation. The extent of the reactive perceptive field for prey was measured from cine photographs and expressed as a function of larval length. Feeding success of larvae fed rotifers was determined for the first 21 days of larval life. These estimates were combined to estimate the volume of water searched by larvae per hour, and this estimate and others were used to calculate the density of food required by larvae to meet metabolic requirements. These calculations indicated that the density of food required by larvae just after yolk absorption was up to 37 times that required by older larvae.

In this report I describe the feeding and swimming behavior of the larval anchovy, *Engraulis mordax*, during the first 30 days of larval life. These observations will be combined with results of other studies in a model for estimation of the survival of larval anchovy in the sea. Similar studies of feeding and locomotor behavior have been made on other larval fishes (Blaxter, 1966; Braum, 1967; Rosenthal and Hempel, 1970), and the biology of larval fishes in general has been reviewed by Blaxter (1969).

APPARATUS AND METHODS

Anchovy larvae were reared from the egg using techniques described by Lasker, Feder, Theilacker, and May (1970). The larvae were kept in 500-liter black, fiber glass tanks in noncirculated sea water at 17° to 18°C. They were illuminated by fluorescent lamps and were given a daily dark period of 10 hr with a half hour of dim light preceding and following the dark period. Larvae were fed a variety of organisms ranging from wild plankton to laboratory-cultured brine shrimp, *Artemia salina*, the dinoflagellate, *Gymnodinium splendens*, the rotifer *Brachionus plicatilis*, and the veligers of various species of mollusks (Lasker et al., 1970; Theilacker and McMaster, 1971).

Most of the data in this report will be concerned with larvae younger than 30 days and 15 mm or less in length because larvae in this size range are more easily cultured than older ones. Metamorphosis of *Engraulis* occurs after about 50 to 60 days at 17° to 18°C when the larva is about 40 mm total length.

Visual observations of the feeding and swimming behavior of larvae were made in the 500-liter rearing tanks throughout the 13-hr day. A larva was chosen and all behavioral acts recorded continuously for 5 or more min. Behavioral acts were given a digital code, and the occurrence, duration of acts, and elapsed time were recorded on eight-channel paper tape by operation of a keyboard. The keyboard controlled a motorized paper-tape punch, and the perforated paper tape was computer-processed. Usually hundreds to thousands of larvae were present; thus a different larva was probably observed during each 5-min observation period and consequently each period was treated as an independent set of observations. A total of 447

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sets of observations was made of larvae ranging in age from 0 to 36 days.

Swimming and feeding behaviors were also recorded on motion picture film for subsequent analysis. For cine photography the larvae were placed in round plastic containers 1 cm deep and 8 to 25 cm diameter which had black opaque walls and a transparent bottom. The tank was illuminated from above by a reflector flood lamp operated below rated voltage. A water bath was inserted between the lamp and the tank to prevent heating the water. Light from the lamp was focused with a fresnel lens on the lens of the motion picture camera beneath the tank. The camera arrangement and lighting system was similar to the one used by Baylor (1959) for photographing transparent organisms with infrared radiation. From the position of the camera the subject was silhouetted against an intensely bright background because the light was focused directly on the camera lens. Thus, low sensitivity, high resolution, and high contrast film could be used. Swimming and feeding larval anchovy were photographed with a high-speed camera at 128 fps (frames per second) using AHU microfile film manufactured by the Eastman Kodak Company.[2] Photographic analysis of feeding was restricted to larvae that fed on food particles 100 μ or larger in diameter because I was not able to resolve smaller food particles and still maintain the larvae in a reasonably large photographic environment. Much slower camera speeds—1 to 2 fps—were used to estimate swimming activity.

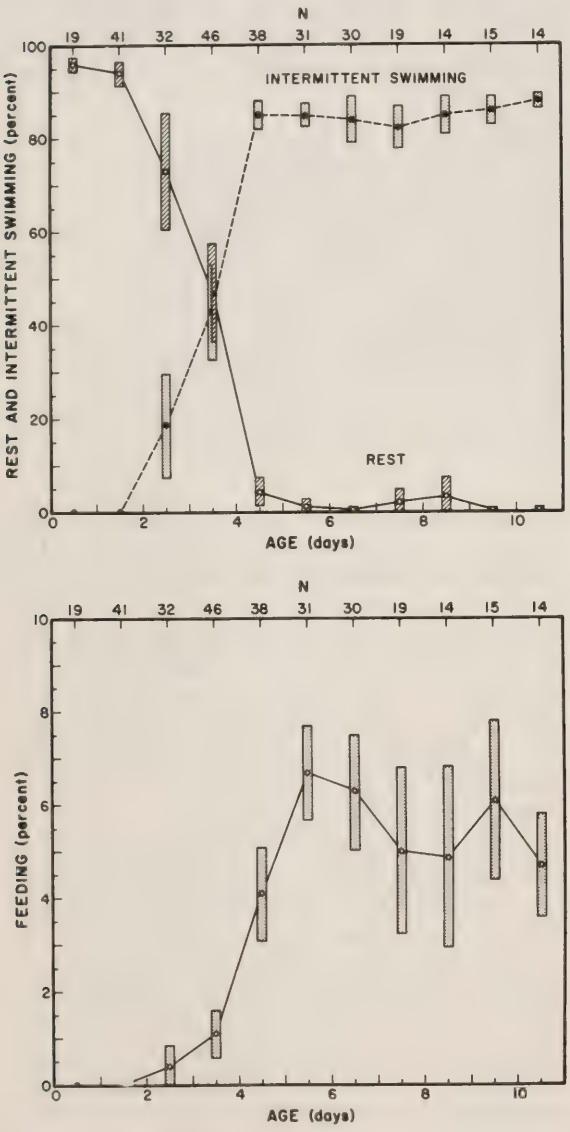

FIGURE 1.—Proportion of time spent in rest and intermittent swimming (top panel), and feeding (bottom panel) by anchovy larvae during the first 10 days of larval life. Points are mean percent $\pm$ 2 $\times$ SE, for each day; the number of observations (N) is given at top of graphs.

SWIMMING BEHAVIOR

CHANGES IN THE TYPE OF SWIMMING WITH DEVELOPMENT

During the first 2 days of larval existence, anchovy larvae exhibited little locomotor activity. Over 90% of the time they floated motionless in the water (Figure 1). Usually the head was directed downward and often the motionless yolk-sac larvae were transported slowly by water currents. Occasionally, they executed a brief but intense burst of swimming. These bursts of swimming, which I called continuous swimming, occurred about once a minute and lasted

[2] Use of trade names does not imply endorsement by the National Marine Fisheries Service.

1 to 2 sec (Table 1). During a burst the tail and body beat continuously from side to side without interruption, and the larva accelerated and decelerated rapidly. Bursts of continuous swimming usually occurred in the absence of any observed stimulus although some bursts were stimulated by accidental contact with other larvae or the walls of the tank.

During the third day of larval life (age 2 days) a new swimming pattern appeared which was to become the dominant mode of locomotion throughout the rest of larval existence. The new mode of swimming was intermittent swimming, consisting of alternate periods of swimming and gliding; typically the larva executed one full tail beat, paused, and glided forward without beating the tail and then repeated the sequence of beating and gliding. The mean proportion of time devoted to intermittent swimming increased during the third and fourth days of larval life, more or less in proportion to the decrease in the time spent in rest (Figure 2). By the fifth day of larval life about 85% of the observation period was composed of intermittent swimming whereas the proportion of time devoted to rest during the day was nearly zero.

With the appearance of intermittent swimming the frequency and duration of continuous swimming decreased. Bursts of continuous swimming occurred once or twice per minute during the first 2 days of larval life whereas by the tenth day they occurred only once in 5 min, and the duration of the bursts also declined over the same period (Table 1). Bursts of continuous swimming occurred at a low frequency throughout the rest of larval life.

TABLE 1.—Proportion of observation time spent in continuous swimming and the mean duration, and mean frequency, of bursts of continuous swimming during the first 10 days of anchovy larval life.

Age days	Percent of observation time Mean ± 2 × SE	Frequency of bursts/min Mean ± 2 × SE	Duration of bursts (sec) Mean ± 2 × SE	N
0	2.4 ± 0.86	0.85 ± 0.28	1.86 ± 0.50	20
1	5.2 ± 0.99	1.72 ± 0.32	1.72 ± 0.48	32
2	2.0 ± 0.58	1.38 ± 0.22	1.38 ± 0.52	28
3	3.4 ± 0.24	0.76 ± 0.78	0.76 ± 0.22	45
4	0.7 ± 0.10	0.33 ± 0.06	0.33 ± 0.16	37
5	0.12 ± 0.16	0.11 ± 0.12	0.37 ± 0.54	32
6	0.16 ± 0.12	0.10 ± 0.22	0.31 ± 0.22	27
7	0.22 ± 0.16	0.18 ± 0.06	0.41 ± 0.26	11
8	0.15 ± 0.18	0.13 ± 0.12	0.23 ± 0.24	13
9	0.29 ± 0.20	0.29 ± 0.18	0.30 ± 0.16	15
10	0.10 ± 0.08	0.20 ± 0.08	0.22 ± 0.14	14

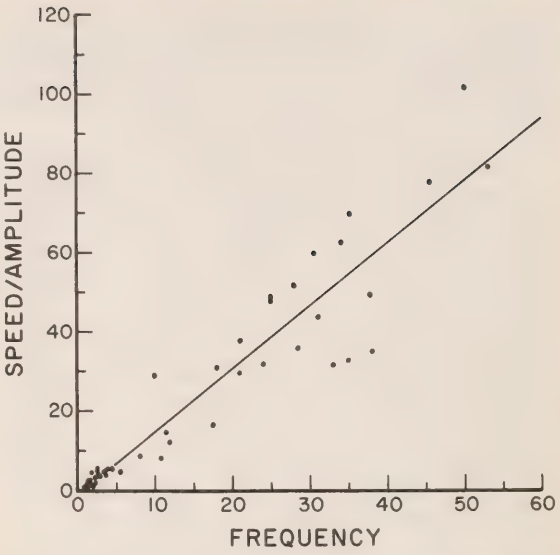

FIGURE 2.—Relationship between speed, tail beat frequency, and tail beat amplitude for anchovy larvae for all types of swimming. Equation for line is $V/A = -1.11 + 1.59\ F$ where V/A is speed (cm/sec) divided by tail beat amplitude (cm), and F is tail beat frequency (beats/sec).

The appearance of intermittent swimming coincided with the appearance of feeding behavior. Feeding behavior was closely associated with intermittent swimming; food was sighted during intermittent swimming and the larvae advanced on the prey using this mode of lomocotion.

POSSIBLE SIGNIFICANCE OE SPONTANEOUS BURSTS OF SWIMMING IN YOLK-SAC LARVAE

The regularity of the bursts of continuous swimming of yolk-sac larvae (age 0-1 day) suggests that the bursts may have a respiratory function. Yolk-sac larvae have no functional gill filaments, and oxygen must be obtained through the integument. Thus the regular bursts of continuous swimming could be necessary for gas exchange. I conducted a short experiment to test this hypothesis.

I measured the duration and frequency of bursts of swimming of age 0 day and 1 day larvae in open 10-liter containers containing water

saturated with oxygen and in ones containing water below saturation at 17°C. In the tests below saturation the initial level was 30% of saturation, but it increased to 65% by the end of the observation period 7 hr later.

At oxygen concentrations below saturation, larvae of both ages swam more frequently than did the controls of the same age ($P \leqslant 0.008$ Mann Whitney U Test, Siegel, 1956). Age 0 day larvae spent 5.36 ± 1.41% (± 2 × SE, N = 15) of the time swimming in water below saturation whereas they spent 1.97 ± 0.64% (N = 10) of the time swimming at saturation. Age 1 day larvae spent 12.48 ± 4.50% (N = 5) of the time swimming in water below saturation whereas the controls spent 3.30 ± 2.31% (N = 5). The proportion of time spent swimming by the controls in both tests did not differ from that given in Table 1 for larvae of the same age.

This experiment suggests that the regular bursts of swimming of yolk-sac anchovy larvae have a respiratory function. On the other hand, the increase in swimming could have been the result of stress induced by low oxygen concentrations and bear no relationship to behavior under normal conditions. I am not inclined to accept this explanation because except for the increase in the duration and frequency of swimming, the behavior of the larvae was normal. A different motor pattern, vigorous shaking of the head, appears at lethal or near lethal levels of oxygen, about 12% of saturation at 17°C.

STRUCTURE OF CONTINUOUS AND INTERMITTENT SWIMMING

To estimate the relationship between larval anchovy tail movement, size, and speed during continuous and intermittent swimming, 53 film sequences were analyzed frame by frame. They included sequences of artificially stimulated and spontaneous bursts of continuous swimming and of bouts of intermittent swimming. In each swimming sequence the mean tail beat amplitude, swimming speed, and tail beat frequency were measured by use of a coordinate reader and digitizer (Hunter and Zweifel, 1971). I assumed that the net course swam was equivalent to a path formed from the midpoints of the tail beat. If the course was straight, this estimate was the same as a regression of the X and Y coordinates for the positions occupied by the head or about the same as a straight line fit by eye through frame by frame tracings of the larva. If the course was curved, the path formed by the midpoints provided a reasonable estimate of the net curvilinear path followed by the larva.

Typically intermittent swimming could be separated from continuous swimming at a glance, but when the tail beat frequency approached that of continuous swimming it was difficult to distinguish between the two types of swimming. Thus, to separate all data into one of the two classes of swimming it was necessary to determine the beat frequency at which larvae changed from intermittent to continuous swimming. This was accomplished by measuring the elapsed time between beats in the slower swimming sequences.

When the tail was beat at a frequency of 4.7 beats/sec or higher, the movement of the tail was continuous, that is, the interval of rest between beats was equal to or less than 0.0078 sec (1 frame at 128 fps). At tail beat frequencies at or below 4.4 beats/sec the movement of the tail was not continuous but rather pauses of 0.086 to 0.811 sec existed between beats. The mean of the duration of rest between beats was 0.30 ± 0.22 sec (±2 × SE) whereas the duration of a single beat was 0.13 ± 0.05 sec. The duration of the pause or glide between beats was independent of larval size or swimming characteristics and was quite variable. The speed of tail movement was also independent of size but was about the same in all larvae. Thus, at beat frequencies below 4 beats/sec, larvae decreased speed by increasing the interval between beats but maintained about the same speed of tail movement.

Continuous and intermittent swimming data (Table 2) were analyzed separately to determine the relationship between tail beat amplitude, speed, length, and tail beat frequency. The general equation $V/A = a + bF$, where A is amplitude in cm, F is tail beat frequency, V is speed in cm/sec, and s_l is the standard deviation about the line, provided the best fit to continuous and intermittent data sets. The intercepts and slopes

for the two data sets were nearly the same, and consequently I combined the data and obtained the relationship of $V/A = -1.11 + 1.59F, s_l = 8.311$ for all data (Figure 2).

The principal difference between the above equation and ones derived by Bainbridge (1958) or by Hunter and Zweifel (1971) for adult fishes was that amplitude was the estimator of size instead of length. Amplitude was required in the present study because during bursts of continuous swimming larvae modulated the amplitude of their tail beat. Inclusion of length in addition to amplitude and frequency did not improve the relationship. In the study by Hunter and Zweifel (1971) fish did not modulate the amplitude of the tail beat because they swam at a steady speed. Amplitude is known to change during acceleration (Gray, 1968), and the behavior of larvae during bursts of continuous swimming was no exception to this rule.

During intermittent swimming, amplitude was not modulated but was maintained at a minimum value of about one-fifth of a body length. The relationship between amplitude and length during intermittent swimming was obtained by the equation $A = 0.112 + 0.170\ L$ where $s_l = 0.066$ (Figure 3).

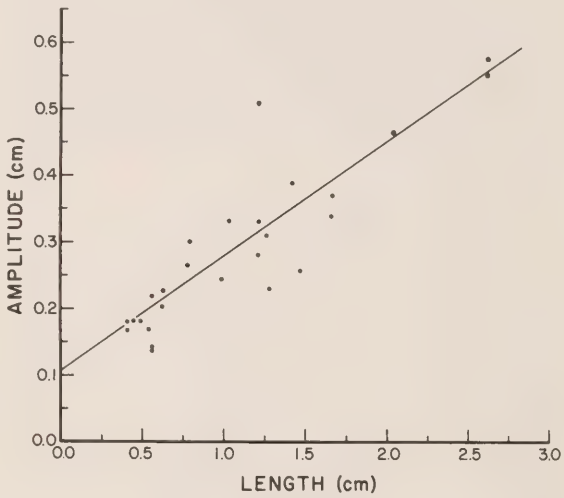

FIGURE 3.—Relationship between anchovy larval length (cm) and tail beat amplitude (cm) for intermittent swimming.

TABLE 2.—The speed, tail beat frequency, and tail beat amplitude for anchovy larvae of various lengths during continuous and intermittent swimming. Each value is a mean for a single swimming sequence swum by one larva.

Continuous swimming				Intermittent swimming			
Length	Speed	Tail beat frequency	Tail beat amplitude	Length	Speed	Tail beat frequency	Tail beat amplitude
cm	*cm/sec*	*beats/sec*	*cm*	*cm*	*cm/sec*	*beats/sec*	*cm*
0.34	4.71	38.1	0.133	0.41	0.31	2.3	0.169
0.37	4.59	33.3	0.142	0.41	0.30	2.0	0.182
0.38	0.75	5.5	0.143	0.45	0.33	2.4	0.183
0.39	10.68	45.5	0.137	0.49	0.20	2.3	0.181
0.41	1.22	10.9	0.150	0.54	0.64	3.8	0.170
0.42	1.08	4.7	0.194	0.56	0.44	2.1	0.221
0.42	8.05	35.3	0.115	0.57	0.73	4.5	0.138
0.42	11.63	50.0	0.114	0.57	0.37	2.7	0.142
0.42	3.86	17.9	0.124	0.62	0.17	1.1	0.205
0.43	7.28	30.5	0.121	0.63	1.01	2.8	0.229
0.43	8.92	34.5	0.140	0.78	0.63	1.3	0.267
0.43	7.91	28.2	0.152	0.79	0.52	1.5	0.302
0.43	7.48	38.5	0.147	0.98	0.20	1.4	0.245
0.44	12.18	53.3	0.148	1.03	1.61	3.1	0.333
0.44	4.89	35.3	0.148	1.21	1.23	2.8	0.514
0.50	9.61	24.7	0.200	1.21	1.35	2.3	0.278
0.56	2.52	17.5	0.150	1.21	1.52	2.6	0.332
0.72	1.75	8.0	0.206	1.27	1.18	2.7	0.310
0.72	2.17	11.4	0.150	1.28	1.27	2.6	0.231
0.93	4.28	10.2	0.148	1.42	1.02	2.1	0.390
1.00	11.22	28.6	0.311	1.47	1.26	3.2	0.257
1.00	15.91	20.7	0.422	1.66	1.02	1.7	0.340
1.24	31.26	31.6	0.716	1.66	0.78	1.7	0.372
1.24	9.08	12.0	0.718	2.04	1.68	2.2	0.468
1.24	23.16	21.0	0.777	2.62	2.50	1.9	0.581
1.32	21.16	24.0	0.664	2.62	3.02	2.9	0.555
1.42	26.85	25.0	0.545				

At intermittent swimming speeds tail movement was slow enough that the frequency of the beat could be counted by eye. If the length of the larva were known, intermittent swimming speed could be estimated from the general speed equation given above, the amplitude equation for intermittent speeds, and the tail beat frequency. Instead of the general speed equation it may be preferable to use one based on intermittent swimming data alone, which is $V/A = 0.0466 + 1.308\ F$ where $s_l = 1.160$.

BURST SPEEDS

The speeds obtained by larval anchovy during bursts of fast continuous swimming are of interest because they may be a measure of the larva's ability to avoid predators or possibly plankton nets. Bursts of fast swimming were stimulated in larvae of mean length 4.1 ± 0.1 mm (Table 2, continuous swimming, 0.34 to 0.44 cm larvae) and mean length 12.1 ± 1.2 mm (Table 2, continuous swimming, 1.00 to 1.42 cm). Bursts were stimulated by moving a pin near a larva and photographing the larva at the film speed of 200 fps. Speeds were averaged for the entire duration of the burst, which lasted about 0.1 to 0.2 sec. The stimulated burst speed for larvae of mean length 4.1 mm was 63 ± 19 mm/sec (mean ± 2 × SE) or about 15 body lengths/sec and that for the 12.1-mm larvae was 198 ± mm/sec or about 16 body lengths/sec. The maximum speed obtained by larvae in the 4.1 mm length class was swum by a 4.2-mm larva which swam 116 mm/sec (28 body lengths/sec) during a burst of 0.12 sec. The maximum speed for larvae in the 12.1 mm class was 313 mm/sec (25 body lengths/sec) swum by a 12.4-mm larva during a burst lasting 0.10 sec. In summary, larvae had a maximum speed capability of 25 body lengths/sec or faster for bursts lasting 0.1 to 0.2 sec, but the typical or average burst speeds were close to 15 body lengths/sec.

ESTIMATES OF DAILY RATE OF SWIMMING

I shall consider only intermittent swimming in the estimates of daily swimming rate because only intermittent swimming was associated with food search, and because once feeding began, continuous swimming was an insignificant proportion of daily activity (Figure 1 and Table 1). Two independent methods were used to estimate the rate of intermittent swimming. In the first method, larvae were photographed at 2 fps in a cylindrical chamber of 25 cm diameter, and swimming speed calculated from frame-by-frame analysis of the photographs. Five minutes of swimming were analyzed for each larva; swimming was divided into intermittent and continuous types; and periods of inactivity equal to or greater than 5 sec were tabulated as rest. In the second method, visual observations of larvae in the 500-liter rearing tanks were used to record the tail beat frequency of larvae during intermittent swimming and the frequency and duration of continuous swimming and rest. Larvae were observed three or more times a day. The speed of larvae during intermittent swimming was calculated from the tail beat frequency by use of the relationships between age, length, amplitude, tail beat frequency, and speed previously described.

The speed of intermittent swimming measured from photographs increased with larval length (Figure 4), and the regression of speed on length gave the relationship $V = -0.215 + 1.038\ L$ where $s_l = 0.280$. Visual measurements of tail beat frequency of intermittent swimming

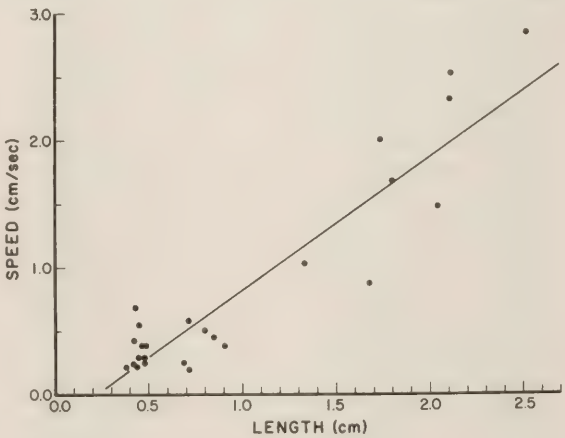

FIGURE 4.—Rate of movement during intermittent swimming (cm/sec) as a function of anchovy larval length (cm). Measurements taken from analysis of cine photographs. Equation for line is $V = -0.215 + 1.038L$.

TABLE 3.—Comparison of visual and photographic estimates of speed of intermittent swimming for anchovy larvae of three sizes.

Larval length (cm)	Tail beat amplitude[1] (cm)	Intermittent speed estimates (cm/sec)		Distance traveled[4] (m/hr)	
		Visual[2]	Photographic[3]	Visual	Photographic
0.5	0.197	0.414	0.304	12.3	9.0
1.0	0.282	0.592	0.823	17.6	24.5
1.5	0.367	0.771	1.342	22.9	39.9

[1] Estimated from $A = 0.112 + 0.170L$.
[2] Estimated from $V/A = 0.047 + 1.308F$, where $F = 1.57$.
[3] Estimated from $V = -0.215 + 1.038L$.
[4] When 82.6% time spent swimming.

did not change with age over the first 30 days of larval life. That tail beat frequency did not change implied that the interval of rest between beats, the principal determinant of frequency, was dependent on variables unrelated to size or development. The same conclusion was obtained from analysis of the structure of intermittent swimming in the preceding section. Thus, the change in speed associated with increased length or age may be a function of only the increase in tail beat amplitude with length.

The mean tail beat frequency for intermittent swimming, 1.57 ± 0.03 beats/sec, was substituted into the speed equation for intermittent swimming. Speed of intermittent swimming could then be determined for larvae of any length by substitution of the appropriate tail beat amplitude into the equation. Speed estimates in which the above procedure was used and ones based on photographic analysis are compared in Table 3. The two sets of estimates are reasonably close for 0.5-cm larvae but they diverge for larger ones. No reason exists to disregard either set of estimates. It seems reasonable to assume that the true values lie somewhere between them.

The proportion of daylight hours devoted to intermittent swimming must be considered to estimate the distance traveled per hour. Visual observations are preferable for this purpose because of the greater number of observations (318) and because visual observations were systematically taken at different times of day. Between ages 4 and 30 days, no trend with age existed in the proportion of time devoted to swimming although time spent swimming decreased slightly on days of intensive feeding. The mean proportion of time devoted to intermittent swimming was 82.6 ± 1.2%. To arrive at this estimate I considered periods of inactivity longer than 5 sec as rest and periods equal to or less than 5 sec as a part of intermittent swimming bouts. Estimates of the distance traveled per hour, assuming 82.6% of the time is spent swimming, are shown in Table 3. These values will be combined with others to estimate rate of food search in a later section.

FEEDING BEHAVIOR

DESCRIPTION OF FEEDING BEHAVIOR

After a larva sighted a prey, the head turned toward it so that the prey was perpendicular to the tip of the snout and thus in about the center of the binocular field of the larva. Then, while keeping the prey in the center of the binocular field, the larva swam slowly toward the prey by executing one or more tail beats. After swimming ceased, the larva contracted its body into an S-shaped striking posture typical of the larval clupeoid fishes (Figure 5). During contraction of the body, the prey was maintained directly in front of the snout and small movements by the prey were compensated for by slight adjustments in the orientation of the head and larger movements by rotating the entire body with the pectoral fins. The larva continuously moved toward the prey while forming the strike posture by high frequency (50 to 60 beats/sec), low amplitude vibration of the finfold or caudal fin.

The order and rate at which portions of the body were contracted to form the S-strike posture were not fixed. The order appeared to be related to the initial orientation of the head and trunk. Frequently swimming movements were integrated into the beginning of the strike posture. The larva while approaching a prey often ceased swimming with the body partially bent, and the contractions to form the strike posture were carried onward from that point. Variations in the rate of contraction were related to movements of the prey. If the larva did not keep up with a moving prey, contraction of the body was often interrupted and the incomplete posture held for an extended period. The ampli-

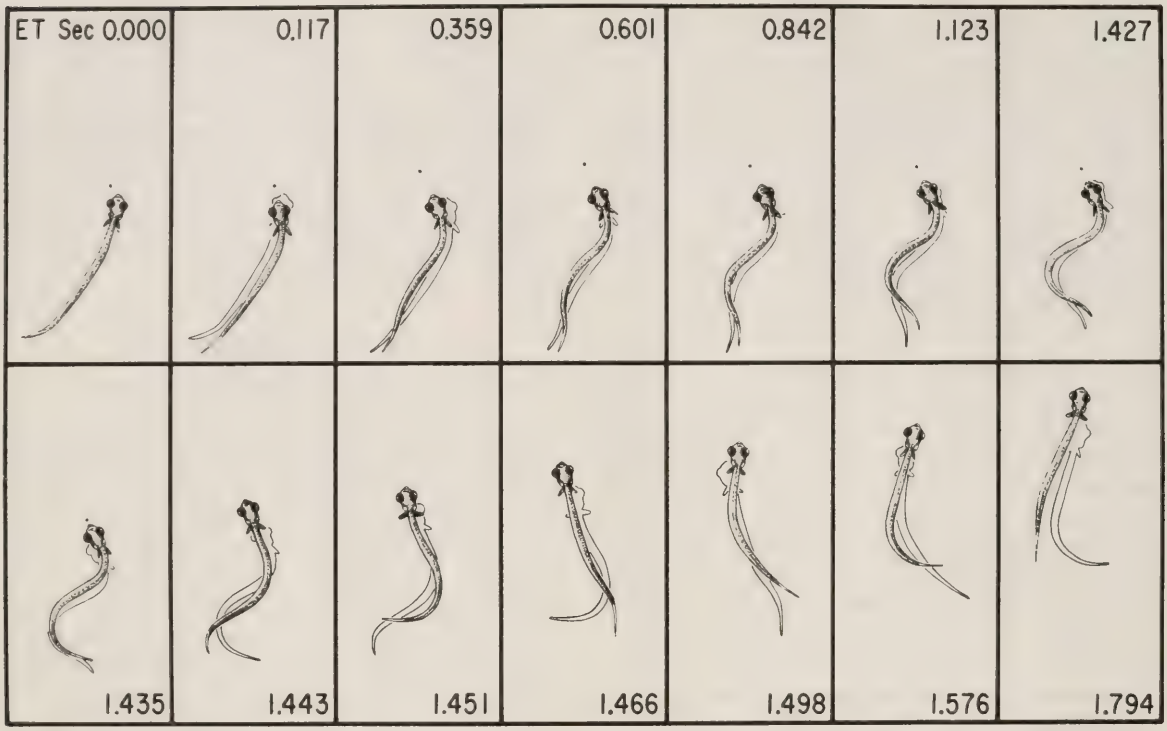

FIGURE 5.—Tracings of selected motion picture frames from a feeding sequence of an anchovy larva (8.9 mm, 21 days old) and a prey taken at 128 frames per second. Frame lines are fixed such that distance moved by larva is indicated by comparison of tracings; and unshaded image indicates position of larva in the preceding tracing. The following events are illustrated: elapsed time (ET) 0 sec, larva sights prey; ET 0-0.117 sec, larva orients head toward prey and swims toward it; ET 0.117-1.435 sec, larva forms *s*-shaped strike posture; ET 1.435-1.443 sec, strike begins and prey captured; and ET 1.451-1.794 sec, forward movement continues as tail returns to axis of progression.

tude of the posterior bend in the body reached a maximum just before the strike was begun.

The larva began the strike by drawing the tip of the tail rapidly anteriorly. It then thrust the tail backward, extended the head, opened the mouth, and the particle was taken or missed within 7.8 to 15.6 msec after the beginning of the backward thrust of the tail (one to two frames at 128 fps). The entire feeding sequence from sighting the prey to the strike lasted only 1 to 2 sec. The sequence of movements were so rapid that my first impression was that they were extremely stereotyped. Later, frame-by-frame analysis of film taken at 128 fps indicated that normal variance was associated with every characteristic that could be measured in the films.

Larvae of 15 to 20 mm formed the strike posture in less time than did one 5 to 15 mm long, and consequently, feeding sequences were shorter in larger larvae (Figure 6). On the other hand, the time used to approach the prey before forming the strike posture was about 0.6 sec in larvae of all sizes. Other characteristics increased directly in proportion to length, for example, the maximum amplitude of the body in the strike posture, the distance to the prey at the time of the strike, and the rate of movement toward the prey while in the strike posture. The speed of the strike also increased with length but the relationship appears to be nonlinear. The speed of the strike relative to length was less in the largest size class of larvae.

INCOMPLETE FEEDING SEQUENCES

Feeding sequences often ended before they were completed by execution of the strike. The mean frequency of feeding strikes (the last act in the feeding sequence) for all visual observations for larvae of ages 4 to 27 days was 1.28 ± 0.14 strikes/min (N = 325) whereas that for the orientation movement of the head (the first act in the sequence) was 3.22 ± 0.30. Thus, about 40% of all feeding sequences were completed. The proportion of feeding sequences that were completed did not change with age, but there was some indication that the proportion of incomplete sequences increased when the larvae began to feed on *Artemia* nauplii. This increase in the proportion of incomplete sequences was caused by an increase in the proportion of sequences ended at the first act, the orientation movement of the head. The proportion of feeding sequences that were carried as far as bending the body was 52% and remained about the same regardless of age or food type.

In the film analysis I analyzed only incomplete feeding sequences that were continued beyond the head orientation movement and compared them with completed sequences. These measurements indicated that some feeding sequences ended at every stage up to and including the final strike posture, and the duration of incomplete sequences overlapped that of completed ones (Table 4). The only characteristic measured in the photographs that consistently separated incomplete from completed feeding sequences was that at the end of incompleted ones the prey was farther away from the larvae than it was in completed sequences. Thus, the principal cause of the failure to continue a feeding sequence was an inability to closely approach the prey while forming the strike posture.

To summarize, photographic analysis of incomplete and complete feeding sequences indi-

TABLE 4.—Comparison of characteristics of incomplete and complete feeding sequences for larval anchovy 5.1-10.0 mm.

Characteristic	Incomplete sequence[1] Mean ± 2 × SE	Complete sequence[2] Mean ± 2 × SE
Duration of S-posture (sec)	0.82 ± 0.26	1.11 ± 0.16
Duration entire sequence (sec)	1.38 ± 0.40	1.71 ± 0.26
Body amplitude (mm)	1.03 ± 0.40	1.52 ± 0.20
Distance to prey at end of sequence (mm)	0.81 ± 0.17	0.41 ± 0.04
S-posture forward movement (mm/sec)	0.51 ± 0.26	0.80 ± 0.34

[1] N = 19.
[2] N = 13.

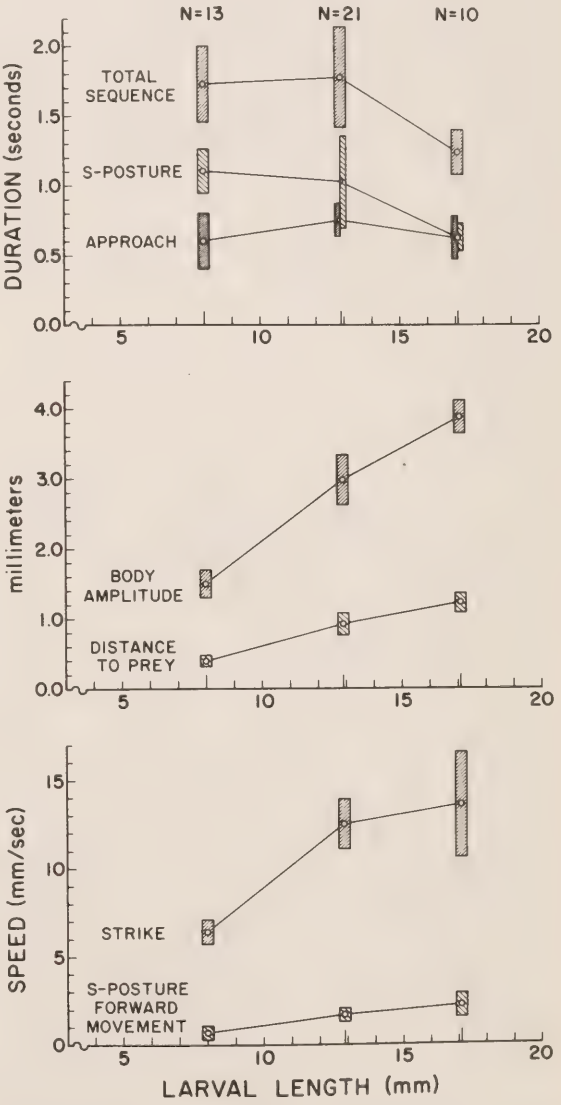

FIGURE 6.—Characteristics of complete feeding sequences of anchovy larvae taken from film analysis. Values are means ± 2 × SE for three size classes of larvae (5.1-10.0, 10.1-15.0, and 15.1-20.0) and are plotted at the mean length of the larvae in the class.

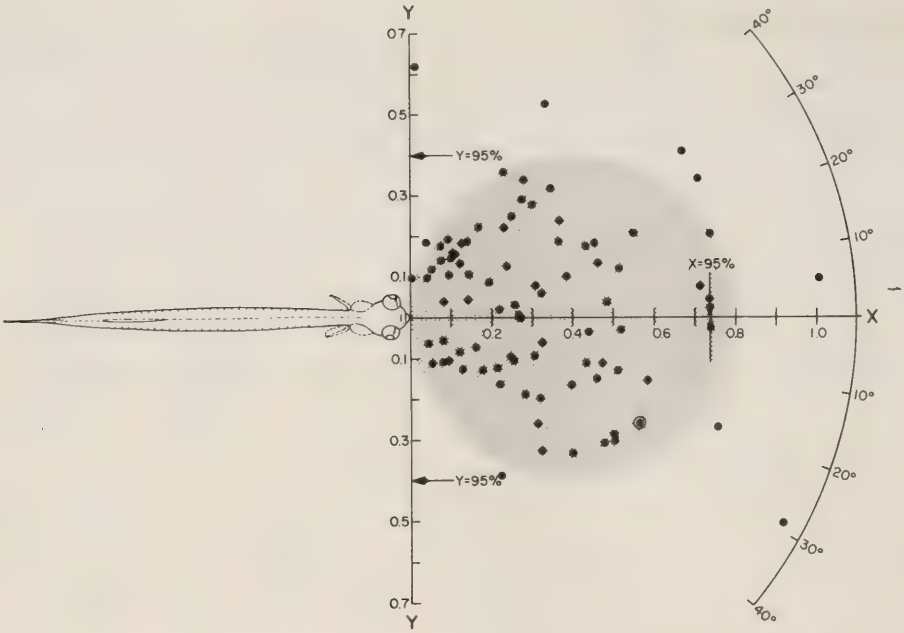

FIGURE 7.—Reactive perceptive field in the horizontal plane for anchovy larvae. Each point represents position of a prey in the horizontal plane at time larvae first reacted to it. Distances in X and Y axes were divided by the lengths of the larvae and expressed as proportions of larval length. Arrows indicate lines that would enclose 95% of prey sighted in each plane.

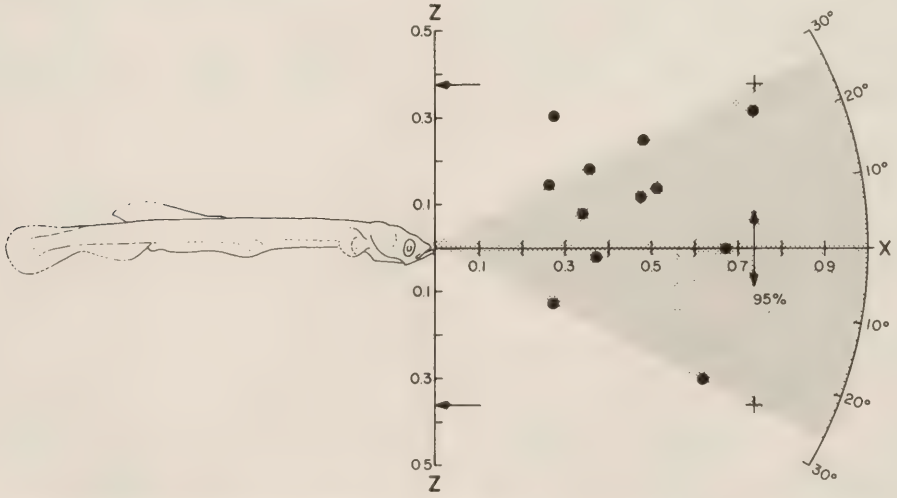

FIGURE 8.—Reactive perceptive field in the vertical plane for anchovy larvae. Distances on X and Z are expressed as a proportion of larvae length; points are position of prey when larvae first reacted to them; crosses indicate point of intersection of visual cone with $Y = 95\%$ (the 95% limit of prey distribution in Y given in Figure 7); and arrows on Z indicate projected values of Z for intersection points.

cated that considerable flexibility exists in what appeared to be a highly stereotyped feeding pattern. Although a sequence was completed in only 1 to 2 sec, the larvae depend on feedback from the prey throughout the period. The larvae respond to the prey during the sequence by adjusting posture, speed, and direction of movement and by ending or continuing the sequence.

EXTENT OF REACTIVE PERCEPTIVE FIELD

The size of the predator's reactive perceptive field (Holling, 1965) is an essential element in the estimation of the rate of search for prey by a predator, that is, the extent of the area in which a predator will react to a prey. In studies on larval fishes the cross-sectional area of the perceptual field is multiplied by the speed of swimming to estimate the volume of water searched per unit of time. Estimates of this type have been made by Braum (1967), Rosenthal and Hempel (1970), and Blaxter (1966) and are summarized by Blaxter (1969).

To determine the position of prey when larvae first reacted to them feeding, larvae were filmed from below for horizontal measurements and separately from the side for measurements in the vertical plane. Seventy-one horizontal film sequences of larvae, 4.0 to 24.2-mm, and 12 vertical sequences of larvae, 7.0 to 24.7 mm, were analyzed frame by frame.

In the film analysis all measurements were made in reference to the body of the larvae; X signified measurements made in the axis of progression or swimming plane; Y those in the other horizontal axis; and Z those made along the vertical axis. Vertical measurements were made in relation to the orientation of the larvae and were not necessarily vertical in relation to the water surface. Searching behavior was independent of body orientation. Larvae reacted to prey when they swam upward, when they swam downward, as well as when they swam parallel to the water surface.

In each photographic sequence the angle and distance of the prey from the tip of the snout of the larva were measured 15 msec before the larva reacted to the prey by turning the head toward it (two frames at 128 fps). To correct for obvious length-dependent differences in field size the distance to the prey was divided by larval length and was expressed in body lengths (L). Prey organisms included *Brachionus*, various veliger larvae, *Artemia* nauplii, and wild copepod nauplii of undetermined species.

In the horizontal plane larvae reacted only to prey ahead of them; prey at 90° or more from the tip of the snout were not selected, and most prey were less than 60° from the snout (Figure 7). The reactive perceptive field in horizontal cross section was roughly circular. A circle of radius $0.4L$ with the center on the axis of progression or X axis enclosed 90% of all prey sighted (shaded area, Figure 7). In the vertical plane, larvae reacted to prey below as well as above the X axis. The maximum distance above and below the X axis at which prey were sighted in the vertical plane was $0.3L$ and thus the maximum extent of Z was $0.6L$ (Figure 8). The reactive perceptive field may be roughly triangular in vertical cross section, because a triangle with a central angle of 53° and altitude of $0.74L$ enclosed all but one of the 12 observed values.

Maxima seem appropriate rather than averages to estimate the extent of the reactive perceptive field because only the exceptional larva survives in nature and because field size may change with feeding motivation. Considering the two axes in the horizontal plane separately, for 95% of all prey sighted the value Y for the position of prey was equal to or less than $0.4L$ from the axis of progression (X axis), and for 95% of all prey the X values for prey position were equal to or less than $0.74L$. Ninety-five percent limits could not be used to estimate Z because the observations were too few to calculate percentages. The maximum observed Z value above and below the X axis was $0.3L$. This value could be used or alternatively Z could be estimated at a point on X by assuming the field is triangular in cross section as illustrated in Figure 8. Using the 95% limit for X, $0.74L$, as the point to make the cross section, we obtain an estimate of $Z = 0.36L$. Thus, the estimate of the maximum extent of Z varied from 0.30 to $0.36L$ depending on the assumptions used. Assuming an elliptical cross section where $Y = 0.40L$ and $Z = 0.36L$ the area of the ellipse is

equal to $0.45L^2$ for a cross section at $X = 0.74L$. To estimate the volume search per unit time these areas need to be multiplied by the larval swimming speed. This aspect of the calculation will be considered in a subsequent section.

FEEDING RATES

In all studies in this paper larvae were observed and maintained in tanks containing high and presumably optimum food densities (*Gymnodinium* 100 to 200/ml, *Brachionus* 10 to 20/ml, and *Artemia* nauplii 3 to 10/ml). It is unlikely that density limited the rate of feeding under these conditions. Thus, the rates recorded probably are near the maximum feeding rate that can be sustained by larval anchovy.

Records were kept of the frequency of feeding acts of larvae ages 4 to 27 days raised in the 500-liter rearing tanks. A total of 325 observations of 5-min duration was taken at three different times of day. No trend in the frequency of feeding strikes with time of day existed. The larvae fed actively throughout the day although their guts were filled after the first half hour of feeding each morning. The average frequency of feeding strikes for all data combined was 1.28 ± 0.144 strikes/min. Some evidence existed that the rate may climb to 3 strikes/min for 2 to 3 days when *Artemia* nauplii were first introduced, but no direct cause and effect relationship could be established because other prey were also present in the tank.

Another estimate of feeding rate was obtained from the data on feeding success described in the next section. The larvae in that study had empty guts at the beginning of the observation period, and they were observed during their initial 10 min of feeding on a particular day, whereas the preceding data observations were begun about a half an hour after the larvae began feeding and continued throughout the day. The average feeding frequency for larvae studied in the feeding success experiments ($N = 100$) was 1.75 ± 0.205 strikes/min and the range was from 0.2 to 5.8 strikes/min. Thus, during the first 10 min of feeding, feeding rates were on the average somewhat higher than they were when averaged over the entire day. Feeding rates on *Artemia* were the same as those on *Brachionus*.

FEEDING SUCCESS

Feeding success was estimated by counting the number of feeding acts completed in 10 min, removing the larvae from the container, and counting the number of prey in the gut. Larvae were kept in the dark for 12 or more hr before the test to insure that the gut was empty (anchovy larvae do not feed in the dark). I measured the feeding success of larvae fed *Brachionus* (density, 10 to 60/ml) from the first day of feeding (age 3 to 4 days) up to the 21st day of larval life. A separate experiment was run to determine the effect of a different prey on feeding success. At age 17 days the diets of some of the larvae were changed from one of only *Brachionus* to one of *Artemia* nauplii (density, 3 to 15/ml). Measurements of feeding success were made over the first week of feeding on *Artemia*. *Gymnodinium* was not used as a food for first feeding larvae because it was usually defecated before we were able to examine the contents of the gut. Two measurements of feeding success of larvae fed *Gymnodinium* fell within the scatter for *Brachionus* (Figure 9).

The success of larvae fed *Brachionus* rapidly increased over the first week of feeding (age 3 to 10 days), but thereafter the rate of increase of feeding success was much lower. The form of the relationship between age and success was that of a learning curve. A semilog transformation of the data provided an adequate correction for this curvilinear trend. The regression of feeding success in percent on the log of larval age gave the relationship, percent success = 93.2 (log age) — 33.30 where $s_t = 20.14$.

Seventeen-day-old larvae were less successful in capturing *Artemia* for the first time than they had been in capturing *Brachionus*. Only 37% of feeding acts were successful when larvae were fed *Artemia* nauplii for the first time at age 17 days whereas 81% were successful when the food was *Brachionus* (Figure 10). The initial level of feeding success for larvae fed *Artemia* was higher than that of larvae when they first began to feed at age 3 to 4 days, and less time was required to obtain a high level of success on *Artemia* than was required for first feeding larvae. By the third day of feeding on *Artemia*

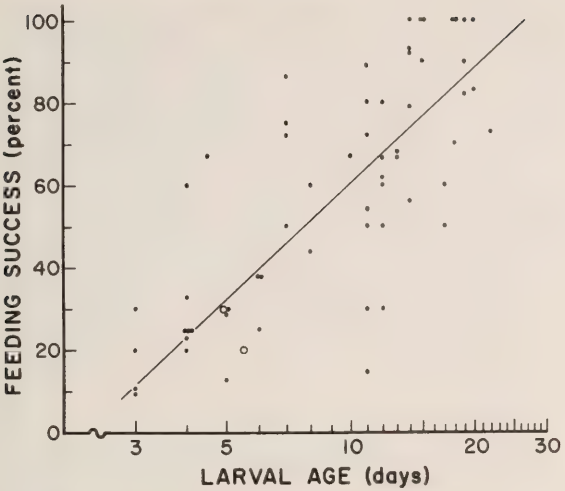

FIGURE 9.—Feeding success (percent of prey captured) of anchovy larvae of various ages fed *Brachionus*. Larval age is plotted on log scale, equation for line is percent success = 93.2(log age) − 33.30. Two open circles, larvae fed *Gymnodinium*.

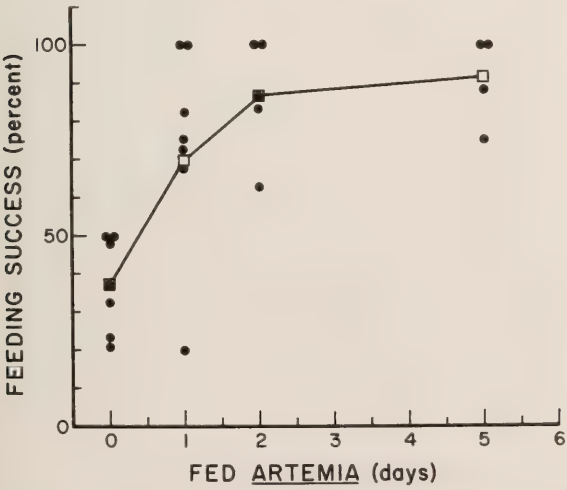

FIGURE 10.—Feeding success of anchovy larvae fed *Artemia* for the first time at age 17 days (0 days on abscissa) and for 5 additional days. The line connects mean values.

the level of success had reached the same level as it had after 2 weeks of feeding on *Brachionus*.

One interpretation of these results is that a considerable proportion of feeding experience on one type of prey is transferable when larvae feed on a new prey. On the other hand, the surprisingly long period (about 2 weeks) required to achieve a high level of feeding success on *Brachionus* suggests that maturation of sensory and locomotor systems may also play a role in anchovy larval feeding behavior during the first 2 weeks of larval life.

ESTIMATION OF VOLUME SEARCHED

In this section I combine the estimates made in the previous section to estimate the volume of water searched by larvae per hour and will use this estimate and others in a subsequent section to calculate the density of food required by larvae to meet metabolic requirements.

The volume of water searched per hour by larvae was calculated by multiplying the cross-sectional area of the reactive perceptive field by the distance traveled per hour by larvae. I made separate calculations for the photographic and the visual speed estimates given in Table 3. In both calculations the speed estimates were adjusted for the proportion of time spent swimming, 82.6%, and they were extended from distance/sec to distance/hr. In this and all subsequent calculations I have made larval age and length interchangeable by using the growth equation $l_t = 3.24e^{0.0555t}$ given by Kramer and Zweifel (1970) who reared anchovy larvae at 17°C under conditions similar to those used in this study.

The estimate of the volume of water searched per hour increased exponentially with size (Figure 11). The two volume estimates were close for larvae less than 10 mm long but they diverged for larger ones. There was no reason to select one estimate over the other and, consequently, I chose to use the average of the two for future calculations. When the two estimates are averaged the outcome is nearly the same as the relationship, volume searched/hr = $1{,}000L^3$, where L is larval length in cm and volume is in cm^3, or simply, liters searched/hr = L^3. Examination of Figure 11 shows the line for L^3 falls almost midway between the two estimates. I shall use the average estimate in the rest of the calculations, but L^3 could be used with only a negligible difference. In the larger larvae L^3

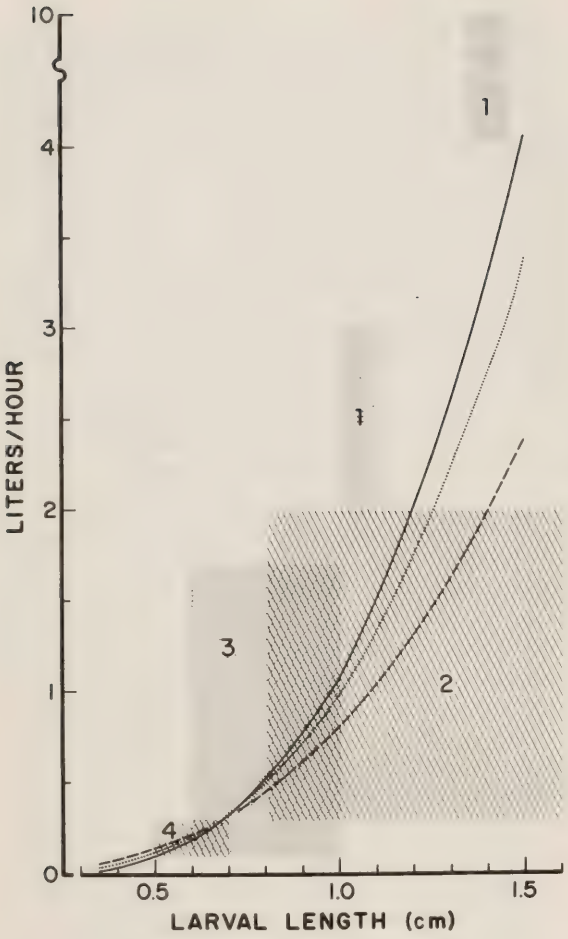

FIGURE 11.—Estimates of liters/hour searched by anchovy larvae 0.3-1.3 cm total length. Lines are based on average estimates and are not data points. Solid line is the volume searched when the photographic estimate of swimming activity was used; dashed line, the volume searched when visual estimate of swimming activity was used; and dotted line, the relationship, liters/hour = L^3, where L is total larval length (cm). Rectangles enclose estimates of search rates for other larval fishes from the literature: 1) *Clupea* (Rosenthal and Hempel, 1970); 2) *Clupea* (Blaxter, 1969); 3) *Pleuronectes* (Blaxter, 1969); and 4) *Sardina* (Blaxter, 1969).

yields a slightly higher estimate than the average estimate, but the difference does not exceed 5% even in the largest larva under consideration.

That the change in volume searched with length was nearly proportional to L^3 could be expected. The volume is the product of the speed and cross-sectional area of the perceptive field for prey. I assumed a length coefficient of one in the calculation of cross-sectional area (area = $0.45L^2$), and the length coefficients for the two swimming speed estimates were close to one as is commonly the case in swimming speed studies (Bainbridge, 1958; Hunter and Zweifel, 1971). Thus the product of the length coefficient for speed and the one for area would be expected to be close to L^3. On the other hand, that the product of the various constants used in the calculation was close to 1,000 was simply chance.

The estimates of volume searched made for other larval fishes, shown as rectangles in the figure, are close to the two for anchovy, especially when the variance in such estimates is considered. How much of the difference between anchovy and other species can be attributed to specific differences and how much to differences in technique and assumptions is unknown. For example, differences in techniques of estimation of the distance of prey at the time of sighting could account for the differences between my results and others. The initial movement of the head toward the prey was easily detected in the films, but it is possible that a significant period elapsed between recognition and movement of the head. If this is true, I have underestimated the size of the perceptive field for prey. Perhaps some of the herring estimates are higher than the anchovy because the anchovy swims more slowly. Anchovy swim more slowly because unlike most pelagic fishes the anchovy swims intermittently; that is they glide between beats of the tail.

ESTIMATION OF FOOD DENSITY

To fulfill their metabolic requirement larval anchovy must ingest about 686 rotifers/day/mg dry weight or the caloric equivalent. This estimate was derived from the following: 4.5 μliter of O_2/mg dry wt/hr is consumed by anchovy larvae kept on a 14-10 hr light-dark cycle (Lasker, personal communication); 1 μliter O_2 = 0.005 cal; caloric value of the rotifer (*Brachionus*) = 5,335 ± 139 cal/g (Theilacker and Mc-

Master, 1971); dry weight 1 rotifer = 0.16 μg of which 92.2% is organic material (Theilacker and McMaster, 1971); and the assumption of 100% digestive efficiency. The estimate was converted from unit weight to length by the length-dry weight relationship of log W = 3.3237 log L — 3.8205 given by Lasker et al. (1970).

The metabolic requirement given above was adjusted for feeding success by increasing it in proportion to the number of prey missed during feeding as predicted by the feeding success equation presented previously. The density of food required for survival was estimated by dividing the food requirement adjusted for feeding success by the volume of water searched in 10 hr. The average of the photographic and visual estimates of volume searched was used to calculate the volume searched by larvae. A 10-hr feeding period was chosen purely as a convenience because the actual duration of daily feeding periods is unknown.

The density of rotifers required to meet metabolic requirements decreased exponentially with size (Figure 12). First feeding larvae, 3 days old (3.5 mm) require 105 rotifers or the caloric equivalents/liter during a 10-hr feeding period whereas 10-day-old larvae (5.9 mm) require only 34 rotifers/liter. Older larvae require much lower food densities primarily because feeding success increases exponentially with age.

Density estimates based on rotifer equivalents probably underestimate the prey density required during the first few days of feeding because a smaller prey is needed by most anchovy larvae during this time. For example, Theilacker and McMaster (1971) found that only 12% of anchovy larvae survive to 19 days old when *Brachionus* was the only food, whereas 40 to 50% survived if in addition to *Brachionus* the dinoflagellate, *Gymnodinium*, was present during the first few days of feeding. To obtain a better estimate of food density required by larvae during the first days of feeding I estimated the caloric value of a single *Gymnodinium* cell and recalculated the density required in terms of dinoflagellate equivalents. The caloric value of a single *Gymnodinium* cell was estimated from the carbon content (Mullin and Brooks, 1970) and by assuming that the carbon content

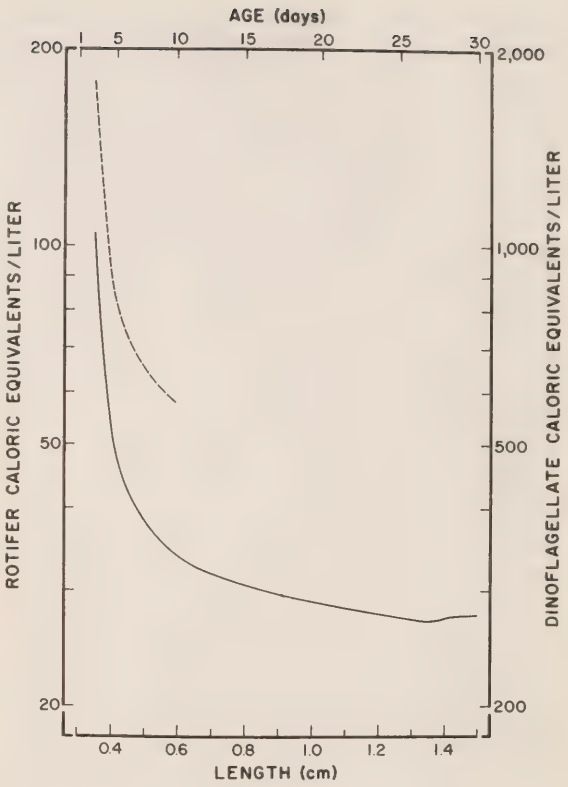

FIGURE 12.—Estimate of the density of prey in rotifer caloric equivalents/liter (left ordinate, solid line) and in dinoflagellate equivalents (right ordinate, dashed line) required to meet metabolic requirements of larval anchovy of 0.3-1.5 cm. Lines are based on average estimates. The shapes of the two curves are the same, but they differ in elevation by a constant factor of 17.

represented 40% of the organic material and that the caloric value of *Gymnodinium* was 5,000 cal/g of organic material. According to this calculation the caloric value of a single *Brachionus* is about 17 times that of a single *Gymnodinium* cell. Thus larvae feeding on dinoflagellates require about 17 times the prey density (dashed line Figure 12) than do those feeding on rotifers (solid line). Nearly all larvae are able to feed on *Brachionus* by age 5 days; thus, the food density requirement for the majority of the larvae shifts from 1,790 dinoflagellates/liter at age 3 days (the first day of feeding) to 48 rotifer equivalents/liter at age 5 days.

Although there are some differences, most of the assumptions and procedures I used were similar to those used by Rosenthal and Hempel (1970) to estimate food densities required by herring larvae. Rosenthal and Hempel estimated that the minimum food ration for herring larvae 10 to 11 mm was 4 to 8 nauplii/liter and the maximum was 21 to 42/liter. My minimum estimate based on metabolic considerations for a comparable size anchovy larvae was 29/liter. For the minimum density they assumed, as I have, that the larva struck at all prey that entered its perceptive field, but for the maximum density they assumed that only a part of the plankters perceived resulted in a completed feeding sequence. In the anchovy larvae feeding on food at high density, on the average only 40% of feeding sequences were completed. Thus, using a similar criterion for a maximum ration as Rosenthal and Hempel (1970), the maximum density required for anchovy larvae would be 2.5 times the minimum ration or for a 10- to 11-mm larva about 72 rotifer equivalents/liter. Considering specific differences and the differences in assumptions and procedures, the estimated food requirements of herring larvae by Rosenthal and Hempel (1970) do not differ much from the one calculated for an anchovy larva of comparable size.

In a survey of the literature given by Blaxter (1965) the densities of food for larval cluepoid fishes in the natural environment ranged from 1 to 68 items/liter. Arthur (1956) in a comprehensive study of the food of pelagic larvae in the California Current region found 1 or more nauplii/liter in 72% of his samples and 30 or more nauplii/liter in about 3% of his samples. Beers and Stewart (1967) measured the density of copepod and naupliar and post naupliar stages (35 to 103 μ) in a 600-mile transect in an area of anchovy abundance and obtained densities ranging from 5 to 17 copepods/liter. Thus, food in the natural environment appears to be near or below the minimum concentration I estimated was required for older larvae but considerably below that for first feeding larvae.

Nearly every adjustment that could be made in my estimates of food requirements for anchovy larvae would sharpen the differences between early and late larval stages or elevate the overall food requirement. For example, natural prey would be of greater variety and could be more difficult to capture, thus causing a differential increase in food concentration required by younger larvae. In addition, older larvae are capable of feeding on a greater variety of food because they can feed on all food used by younger stages plus larger prey as well. I assumed a digestion efficiency of 100% but it must be less than that and this would also increase the overall food requirement. In short, an adjustment in the estimates would probably increase the difference between the estimated food density requirements taken from laboratory measurements and natural food densities.

Laboratory measurements indicated that larval anchovies are more vulnerable to death from starvation just after yolk absorption than at any other time during larval life. This conclusion agrees with those drawn from similar laboratory studies on the herring and other species. Whether or not the increased vulnerability to a starvation death just after yolk absorption is related to year class strength as contended by Hjort (1914) is still a debated question (Blaxter, 1969; Saville, 1971). The catch curves for larval anchovy over 10 years give no indication of an increase in mortality just after yolk absorption (Lenarz, 1972). Three explanations for the absence in the anchovy of an early critical period are: first, turbulence may generate random movement between fish larvae and prey and thereby considerably extend the search volume (Murphy, 1961); second, it may be that the mortality of larvae at all stages is so great because of starvation and other causes that the increased vulnerability at the youngest stages is not detectable; and third, food may not be limiting for early larvae because of patchy food distribution. The absolute number of prey required by early anchovy larvae is not great but a high concentration is required; hence, the patch size could be quite small. It would be of interest in this regard to determine the size, density, and distribution of food patches in the natural environment on a scale appropriate to fish larvae. It would also be of interest to determine the

extent larvae are adapted in their searching behavior to a patchy food distribution.

SUMMARY

1. During the first 2 days of larval life (age 0-1 day) anchovy larvae spent 95% of the time resting. Rest was interrupted once a minute by a burst of continuous swimming lasting 1-2 sec. By age 4 days, yolk was completely absorbed; 85% of the time was spent in intermittent swimming, 7% in feeding, and only 4% in rest. The proportion of time spent in each of these activities remained about the same thereafter.

2. Intermittent swimming was associated with food search. It consisted of repeated sequences of a single tail beat followed by a glide. The speed of the tail was a constant; thus, tail beat frequency was a function of the glide duration. During intermittent swimming tail beat amplitude (A) was the constant proportion of length (L) expressed by the equation, $A = 0.112 + 0.170L$.

3. In continuous swimming, larvae executed a burst of swimming in which no pauses existed between tail beats. Both tail beat frequency and amplitude were modulated during the burst because the larvae accelerated and decelerated. Larvae had a burst speed capability in excess of $25L$/sec for bursts lasting 0.1-0.2 sec, but the typical or average burst speed was near $15L$/sec. The speed (V), tail beat frequency (F), and amplitude (A) relationship for continuous and intermittent swimming were expressed by the equation, $V/A = -1.11 + 1.59F$.

4. The daily rate of movement of larvae excluding rest was estimated using visual and photographic techniques. Measurements taken from cine photographs gave the relationship $V = -0.215 + 1.038L$. Visual observations indicated that average tail beat frequency during intermittent swimming was a constant for larvae of different sizes, and this value was used to provide an additional estimate of the daily rate of movement.

5. The size of the reactive perceptive field for larval anchovy was determined from cine photographs taken in vertical and horizontal planes by plotting the position of prey when larvae first reacted to them. The limits of the perceptive field were set to include 95% of the prey sighted. The field was elliptical, and increased with length and had a cross section proportional to $0.45L^2$.

6. Larvae first reacted to prey by turning the head toward the prey. The larvae then swam toward it, stopped swimming, coiled the body into an S-shape, and struck at the prey by thrusting the tail backward and extending the head. The total feeding sequence lasted only 1-2 sec. Throughout the sequence the larva adjusted its body to compensate for movements by the prey and slowly moved toward the prey by vibrating the finfold or caudal fin.

7. Only 40% of all feeding sequences were completed. Sequences were ended at all stages up to just before the strike began. The principal cause of failure to complete a feeding sequence after a larva began to form the S-shaped posture was the inability of the larva to close the distance between it and the prey.

8. Under conditions of high food density, larvae fed throughout the day. The average feeding rate for larvae 4 to 27 days old was 1.28 completed feeding sequences/min. During the initial filling of the gut in the morning the mean rate was to 1.75/min.

9. Feeding success of larvae fed *Brachionus* increased rapidly from 11% success on the first day of feeding (age 3 days) to 50% by age 8 days, but the rate of improvement was more gradual thereafter. The relationship between feeding success and age was expressed by the equation, % success = 93.2 (log age) — 33.30. Seventeen-day-old larvae were less successful in capturing *Artemia* for the first time than they had been in capturing *Brachionus*, but after 3 days of feeding experience on *Artemia* the larvae regained their former level of success.

10. The liters of water searched per hour by larval anchovy were estimated by combining the estimate of the reactive perceptive field with an estimate of sustained swimming activity. When the average of the two swimming activity estimates was used, the estimate of volume searched was nearly the same as the relationship, liters searched/hr = L^3 where L is larval length in cm.

11. The density of rotifers and dinoflagellates required for larvae to meet metabolic needs was

calculated from caloric and respiration data, and estimates of volume searched and feeding success. These calculations indicated that anchovy larvae just after yolk absorption require up to 37 times the food density as older larvae. Thus, just after yolk absorption anchovy larvae are more vulnerable to death from starvation than at any other time during the larval stage.

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David Holts assisted in all but the work on feeding success which Gary Thomas assisted. Alan Good wrote the program used to analyze the swimming behavior of larvae and the one used to analyze observational data collected on paper tape. James Zweifel fit various models to the swimming data.

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MESH RETENTION OF LARVAE OF *SARDINOPS CAERULEA* AND *ENGRAULIS MORDAX* BY PLANKTON NETS

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ABSTRACT

Mesh retention of the standard plankton sampling gear used by the California Cooperative Oceanic Fisheries Investigations between 1949 and 1968 for larvae of the Pacific sardine (*Sardinops caerulea*) and northern anchovy (*Engraulis mordax*) was estimated by comparing catches made by the standard gear with a gear that retains larvae of all sizes. The results indicate that 67% of sardine larvae and 60% of anchovy larvae are retained by the meshes of the standard gear. The standard gear was replaced by a similar gear in 1969. Apparently all anchovy larvae are retained by the new gear. The new gear is the same as the old gear except for the netting. The netting of the new gear is constructed from 0.505-mm mesh width nylon while the netting of the standard gear was constructed from 0.55-mm mesh width silk. Catch curves of anchovy and sardine larvae corrected for escape through meshes revealed no evidence of a critical period.

Although fisheries literature contains numerous examples of estimates of mesh retention of fish by commercial fishing gear, there is little quantitative work on mesh retention of fish larvae by plankton gear. A review of such studies by Vannucci (1968) revealed only three papers containing quantitative estimates of mesh retention by plankton gear. The lack of knowledge on this subject can cause serious errors when comparing the estimates of abundance of fish larvae made from samples taken by different sampling gears or of two or more species of fish larvae by the same gear.

This paper presents estimates of mesh retention of larvae of the Pacific sardine (*Sardinops caerulea*) and northern anchovy (*Engraulis mordax*) by plankton nets that have been used by the CalCOFI (California Cooperative Oceanic Fisheries Investigations). Estimates are made of the errors that result because mesh retention is ignored when the relative abundance of the two species is calculated and when abundance of the anchovy is computed using data from two quite similar types of sampling gear. Finally the catch curves of the two species are examined for evidence of the critical period proposed by Hjort (1926).

Several authors have noted that small larvae of the Pacific sardine and northern anchovy are not completely retained by the meshes of the plankton nets used by the CalCOFI, but did not have the necessary data to make quantitative estimates of the retention rates. Ahlstrom (1954) noted that small sardine larvae were not fully retained by the meshes of the net in use at that time. Ahlstrom (personal communication) attempted to obtain a measure of the retention rates with a series of paired plankton samples made with a regular CalCOFI net and a net with a finer mesh, but failed to capture an adequate number of sardine larvae. Isaacs (1965) concluded that anchovies up to 7.75 mm were not fully retained by the meshes. He attributed differences in the form of catch curves of anchovy larvae in different years to changes in the minimum size of complete retention. Murphy (1966) stated that anchovy larvae are undersampled ". . . by a factor of about 2, relative to sardines, i.e., they tend to pass through the mesh of the net to a marked extent." He did not describe his method of obtaining the estimate but later informed me (Murphy, personal communication) that he based his conclusion on comparison of catch curves with hypothetical curves based on the assumption of exponential mortality. Lenarz (in press) estimated that

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northern anchovy larvae were undersampled by a factor of 3.4 relative to sardine larvae because of differences in retention rate and rate of decline in catch with increase in size. His estimates of retention rates also were based on differences between observed catch curves and hypothetical curves based on a constant rate of decline.

METHODS

The data for this study on fish larvae were taken from CalCOFI plankton tows. From 1949 to 1968, CalCOFI used a single silk net (type 1) of 0.55-mm mesh with a 1-m diameter mouth opening. During 1966-68 this net was paired with one of nylon of 0.333-mm mesh (type 2) with a ½-m diameter mouth opening. In 1969 the netting of the larger net was replaced with monofilament nylon netting of 0.505-mm (type 3). The variance of mesh width of the type 3 net is considerably less than that of the type 1 net. Other details of the net characteristics are available from Smith[2]. The nets were lowered and raised obliquely at a rate of 1.5 knots to a depth of 140 m in 1966-1968 and to 210 m during 1969. Since very few anchovy or sardine larvae occur below a depth of 140 m, the change in depth should make no difference in the results of this study. Other details of sampling are described by Ahlstrom (1966).

All sardine and anchovy larvae in each sample were identified and measured to the nearest 0.5 mm, standard length. The data revealed evidence of varying degrees of personal bias towards favoring measurements of whole millimeter rather than half millimeter. Sette (1950) was aware of the potential for this type of bias in measuring adult fish and stated: "... to avoid personal bias in favor of whole or half centimeter marks, the measuring scale had uniform graduation marks and they were serially numbered. In addition to avoiding bias, this had the advantage of giving two digit numbers for all listings and computations, the data being divided by two for conversion to centimeters at the final stage of work." Perhaps it would be prudent to follow the advice of Sette, if 0.5 mm accuracy is desired. Evidence of personal bias in measuring the smallest sizes of larvae was also noted. Since the smallest larvae are often distorted, it is difficult to make objective measurements. Because of the above described biases, measurements of the larvae are grouped into the intervals shown in Tables 1 and 2. Larvae captured by the type 2 net were multiplied by the ratio of volume of water sampled by the type 1 net to the volume of water sampled by the type 2 net to adjust for the smaller size of the type 2 net. The samples were chosen on the basis of the presence of sardine larvae or moderate numbers of anchovy larvae.

The following equations, using the notation of Regier and Robson (1966), were used to estimate mesh retention of the type 1 net

$$n_{1jk} = S_{1j}n_{2jk} + e_{jk} \qquad (1)$$

where n_{ijk} = number of larvae of size L_j caught by type i net in kth sample.

s_{ij} = mesh retention of type i net to larvae of size L_j, i.e., $s_{ij} = n_{ij}/N_j$

where N_j = either absolute or relative number of larvae of size L_j in the population.

e_{jk} = error term that is assumed to be normally distributed and independent of n_{2jk}.

The use of equation (1) to estimate mesh retention of the type 1 net implies the assumption that s_{2j} is 1 for all j, i.e., $N_j \approx n_{2j}$. Preliminary analysis of data obtained from a series of paired samples of the type 2 net and a finer meshed net indicates that this assumption is valid for northern anchovy and Pacific sardine (P. E. Smith, personal communication). This method of estimating S_{1j} from a known or estimated N_j is noted as the "direct approach" in the terminology of Regier and Robson (1966).

The least squares estimate of s_{1j} is given by Cochran (1963) as

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TABLE 1.—Catches of northern anchovy larvae by type 1 (0.55-mm mesh) and type 2 (0.333-mm mesh) nets for each sample.

Cruise	Station	Net type	Standard length							
			2.5	3.75	4.75	5.75	6.75	7.75	8.75	9.75
6601	93.35	1	141	175	38	18	17	14	4	0
		2	994.950	55.275	22.110	25.795	14.740	0.000	0.000	0.000
6601	103.29	1	95	121	291	145	45	23	10	5
		2	164.250	141.255	351.495	128.115	42.705	22.995	13.140	3.285
6601	120.24	1	22	51	66	62	30	21	15	4
		2	32.330	54.961	109.922	42.029	42.029	32.330	22.631	12.932
6601	120.35	1	25	59	37	17	11	0	0	0
		2	36.113	68.943	36.113	16.415	0.000	0.000	0.000	0.000
6607	113.50	1	3	1	1	1	0	0	1	0
		2	9.716	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6607	117.45	1	0	11	23	22	13	6	6	5
		2	4.448	84.512	44.480	26.688	12.344	4.448	8.896	0.000
6607	118.39	1	17	64	22	9	8	10	14	0
		2	208.518	117.858	13.599	13.599	9.066	4.533	4.533	4.533
6607	119.33	1	96	72	109	126	90	56	33	9
		2	32.508	102.168	130.032	130.032	116.100	55.728	32.508	9.288
6607	120.25	1	8	11	2	2	0	0	0	0
		2	97.196	128.122	26.508	8.836	4.418	0.000	0.000	0.000
6607	133.23	1	1	0	0	0	1	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6607	137.22	1	3	58	217	133	91	45	25	3
		2	8.212	143.710	316.162	176.558	90.332	86.226	36.954	16.424
6607	137.23	1	6	29	41	80	45	27	13	2
		2	66.195	61.782	105.912	52.956	26.478	30.891	8.826	13.239
6608	87.35	1	360	11	13	6	6	8	2	0
		2	877.150	162.190	122.470	33.100	39.720	26.480	6.620	3.310
6608	130.28	1	23	43	21	10	1	1	1	0
		2	29.552	51.716	18.470	0.000	0.000	0.000	0.000	0.000
6608	130.30	1	13	29	29	15	7	1	0	0
		2	47.879	66.294	22.098	11.049	11.049	7.366	0.000	0.000
6608	133.25	1	32	19	7	8	2	0	1	0
		2	151.578	79.398	21.654	25.263	7.218	0.000	0.000	0.000
6610	120.40	1	0	0	0	0	0	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6610	130.28	1	0	5	6	9	2	3	0	1
		2	0.000	7.128	10.692	0.000	0.000	0.000	0.000	0.000
6611	120.25	1	0	0	0	0	0	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6611	137.23	1	32	1	1	0	0	0	0	0
		2	127.575	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6706	83.55	1	9	17	36	53	35	33	23	25
		2	41.808	62.712	70.551	39.195	44.421	23.517	15.678	33.969
6706	110.40	1	21	6	30	57	56	52	48	58
		2	3.074	3.074	24.592	18.444	36.888	12.296	15.370	3.074
6706	120.24	1	1	0	0	4	4	1	0	0
		2	6.278	0.000	0.000	0.000	3.139	0.000	0.000	0.000
6706	120.40	1	2	4	14	31	19	26	12	7
		2	0.000	0.000	17.550	14.625	14.625	20.475	5.850	5.850
6712	107.45	1	123	106	18	10	13	1	5	0
		2	287.586	114.297	11.061	14.748	14.748	0.000	0.000	0.000
6712	120.50	1	333	23	9	11	7	6	1	0
		2	496.110	14.380	0.000	7.190	17.975	0.000	3.595	3.595

$$\tilde{s}_{1j} = \frac{\sum_{k=1}^{m} n_{1jk} n_{2jk}}{\sum_{k=1}^{m} n_{2jk}}, \qquad (2)$$

where m = number of samples.

However, if the assumption of independence of e_{jk} is violated, (2) is not the least squares estimate of s_{1j}. A form of violation of the assumption which is common in plankton sampling is that the error term is proportional to $\sqrt{n_{2jk}}$. In this case the least squares estimate of s_{1j} is given by Cochran (1963) as

TABLE 2.—Catch of Pacific sardine larvae by type 1 (0.55-mm mesh) and type 2 (0.333-mm mesh) nets for each sample.

Cruise	Station	Net type	Standard length							
			2.5	3.75	4.75	5.75	6.75	7.75	8.75	9.75
6601	93.35	1	0	0	0	0	0	0	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6601	103.29	1	0	0	0	2	1	0	0	0
		2	0.000	3.285	3.285	0.000	0.000	0.000	3.285	0.000
6601	120.24	1	1	2	7	8	4	3	0	1
		2	0.000	3.233	16.165	6.466	12.932	0.000	0.000	0.000
6601	120.35	1	0	1	38	4	0	0	0	0
		2	0.000	3.283	42.679	0.000	0.000	0.000	0.000	0.000
6607	113.50	1	0	0	2	8	0	0	0	0
		2	0.000	0.000	4.858	4.858	0.000	0.000	0.000	0.000
6607	117.45	1	0	0	0	2	8	5	5	3
		2	0.000	0.000	0.000	13.344	8.896	8.896	17.792	13.344
6607	118.39	1	0	3	16	17	4	2	0	0
		2	0.000	0.000	31.731	18.132	0.000	0.000	0.000	0.000
6607	119.33	1	0	0	0	0	2	1	0	0
		2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
6607	120.25	1	4	3	4	0	0	0	0	0
		2	13.254	8.836	17.672	0.000	0.000	0.000	0.000	0.000
6607	133.23	1	10	28	8	6	2	0	0	0
		2	43.030	51.636	12.909	21.515	8.606	0.000	4.303	4.303
6607	137.22	1	60	15	8	11	14	6	3	3
		2	147.816	24.636	24.636	32.848	12.318	4.106	8.212	8.212
6607	137.23	1	5	0	1	0	1	1	0	1
		2	0.000	4.413	0.000	0.000	0.000	0.000	0.000	0.000
6608	130.28	1	8	33	29	27	9	5	1	1
		2	36.940	70.186	33.246	33.246	3.694	7.388	3.694	0.000
6608	130.30	1	83	56	15	8	1	0	2	1
		2	99.441	77.343	7.366	11.049	7.366	0.000	3.683	0.000
6608	133.25	1	11	63	13	3	6	0	1	0
		2	43.308	198.495	14.436	10.827	3.609	0.000	0.000	0.000
6610	120.40	1	2	14	9	4	5	8	6	8
		2	0.000	10.761	7.174	3.587	14.348	17.935	10.761	3.587
6610	130.28	1	2	32	2	0	0	0	0	0
		2	7.128	46.332	0.000	0.000	0.000	0.000	0.000	0.000
6611	120.25	1	1	13	263	294	111	75	40	33
		2	3.621	28.968	318.648	152.082	83.283	83.283	65.178	32.589
6611	137.23	1	1	23	2	1	0	0	0	0
		2	10.935	54.675	0.000	0.000	0.000	0.000	0.000	0.000
6706	110.40	1	0	1	9	0	0	0	0	0
		2	0.000	0.000	3.074	0.000	0.000	0.000	0.000	0.000
6706	120.24	1	5	30	57	13	4	1	0	0
		2	113.004	194.618	116.143	12.556	0.000	0.000	0.000	0.000
6706	120.40	1	4	118	175	65	25	11	5	2
		2	32.175	216.450	187.200	35.100	8.775	5.850	2.925	0.000

$$\tilde{s}_{1j} = \frac{\sum_{k=1}^{m} n_{1jk}}{\sum_{k=1}^{m} n_{2jk}}. \qquad (3)$$

Plots of n_{1jk} and n_{2jk} did not clearly indicate the relation between e_{jk} and n_{2jk}. Thus both methods of estimating s_{1j} were used.

Examination of the data revealed that a linear equation is appropriate to describe the relation between s_{1j} and L_j when $L_j \leqslant 5.75$ mm.

$$\tilde{s}_{1j} = a + bL_j. \qquad (4)$$

Linear regression techniques were used to estimate the parameters, a and b, of the equation.

RESULTS

Table 1 presents catches of anchovy larvae by the type 1 and type 2 nets for each sample. The first two digits of the cruise refer to year and the second two by month. Station notation is explained by Ahlstrom (1966). Larvae greater than 9.75 mm were captured, but the numbers involved were too small to be useful for the study. Estimates by (2) and (3) of s_{1j} are as follows:

L_j(mm)	$\tilde{s}_{1j}(2)$	$\tilde{s}_{1j}(3)$
2.50	0.312	0.367
3.75	0.512	0.603
4.75	0.711	0.699
5.75	0.946	1.057
6.75	0.875	0.916
7.75	0.753	1.021
8.75	1.007	1.226
9.75	0.664	1.087

Plots, Figure 1, of the estimates show that there is a very good linear relation between the estimates and L_j when 2.50 mm $\leqslant L_j \leqslant$ 5.75 mm. When $L_j > 5.75$ mm $\tilde{s}_{1j}(2)$ decreases while $\tilde{s}_{1j}(3)$ fluctuates about 1. Thus it appears that a linear relation (4) provides an adequate description of the relation between $\tilde{s}_{1j}$ and L_j when 2.50 mm $\leqslant L_j \leqslant$ 5.75 mm. When $L_j > 5.75$ mm it is assumed that $\tilde{s}_{1j} = 1$. Vannucci (1968) reviewed papers that used the logistic and normal distribution functions which have s_{ij} approaching 1 as an asymptote rather than the discontinuous equation used in this study. The data used in this study are not accurate enough when $L_j > 5.75$ mm to warrant use of an asymptotic relation. The very good linear relation between L_j and $\tilde{s}_{1j}$ when $L_j \leqslant 5.75$ mm and the high values of $\tilde{s}_{1j}$ when $L_j = 5.75$ mm indicate that any deviation from the equation used in this study would cause minor errors when $\tilde{s}_{1j}$ are used to correct catches of anchovy larvae for loss through meshes.

The estimate of a from (2) and (4) is —0.1942, b is 0.1945, and the correlation coefficient, r, is 0.9961. When (3) was used a is —0.1075, b is 0.1850, and r is 0.9814.

Table 2 contains catches of sardine larvae used in the study. Estimates by (2) and (3) of s_{1j} are as follows:

L_j(mm)	$\tilde{s}_{1j}(2)$	$\tilde{s}_{1j}(3)$
2.50	0.375	0.358
3.75	0.385	0.436
4.75	0.817	0.782
5.75	1.754	1.330
6.75	1.275	1.203
7.75	0.881	0.926
8.75	0.584	0.526
9.75	0.873	0.854

The estimates of s_{1j} for sardine larvae are similar to those for anchovy larvae. Thus the same discontinuous function is assumed. The estimate of a from (2) and (4) is —0.2382, b is 0.2107, and r is 0.9320. Estimates obtained when (3) was used are a, —0.2286, b, 0.2084, and r, 0.9639. The resulting curves for both anchovy and sardine larvae are shown in Figure 2. The curves differ little either within or between species. Since the highest value of r, 0.9961, was estimated for anchovy larvae using equation (2), the somewhat arbitrary decision was made to use the results obtained from equation (2).

ESTIMATION OF PORTION OF LARVAE PASSED THROUGH MESHES OF TYPE 1 (0.55-MM MESH) NET

The type 1 net has been the major plankton sampler of the CalCOFI. Estimates of spawning biomass of the northern anchovy population have been based on the ratio of total catches of sardine larvae to total catches of anchovy larvae (Ahlstrom, 1968). If there are major differences in the percentages of sardine and anchovy larvae retained by the net, then the estimates of anchovy spawning biomass may be seriously in error. Ahlstrom (personal communication) believed that his assumption that the two species were sampled equally well was valid because of the similar forms of larvae of the two species and his interpretations of catch curves of larvae of the two species.

Catch (average) curves of anchovy and sardine larvae were calculated from a series of CalCOFI samples taken during the months of January through July during the decade 1951-1960. More than 10,000 samples are involved. Catch curves were calculated for day and night samples separately because of marked differences between the two. The curves were then corrected for nonretention of larvae as follows:

$$n'_{1jko} = n_{1jko}(1/s_{1j}) \qquad (5)$$

where n'_{1jko} = the corrected catch of larvae of size L_j by net type 1 in the kth time of day, and oth species.

$$k = \begin{cases} 1 \text{ for night samples} \\ 2 \text{ for day samples} \end{cases}$$

$$o = \begin{cases} 1 \text{ for anchovy} \\ 2 \text{ for sardine} \end{cases}$$

The corrected and uncorrected curves plotted on a semilogarithmic scale are shown with n_{1jko} and n'_{1jko} expressed in percent of total in Figures 3-6. The corrected curve for anchovy larvae caught at night shows a slight increase in the rate of decline with size. The corrected curve for anchovy caught during the day is essentially linear as is the corrected catch curve for sardine larvae caught during the night. The corrected catch curve for sardine larvae caught during the day shows a decreasing rate of decline with size. In all cases the corrected curves show little indication of undersampling of small larvae.

The following equation was used to estimate the portion of larvae not collected by the type 1 net because of passage through the mesh:

$$P_{1o} = \frac{\sum_{jk} \sum n_{1jko}}{\sum_{jk} \sum n'_{1jko}} \qquad (6)$$

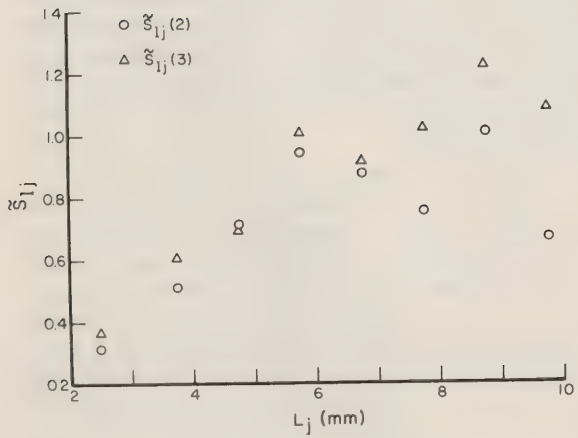

FIGURE 1.—Scatter diagram of estimates of mesh retention by type 1 (0.55-mm mesh) net using equation (2) ($S_{1j}(2)$), mesh retention using equation (3) ($s_{1j}(3)$), and standard length (L_j) for northern anchovy larvae.

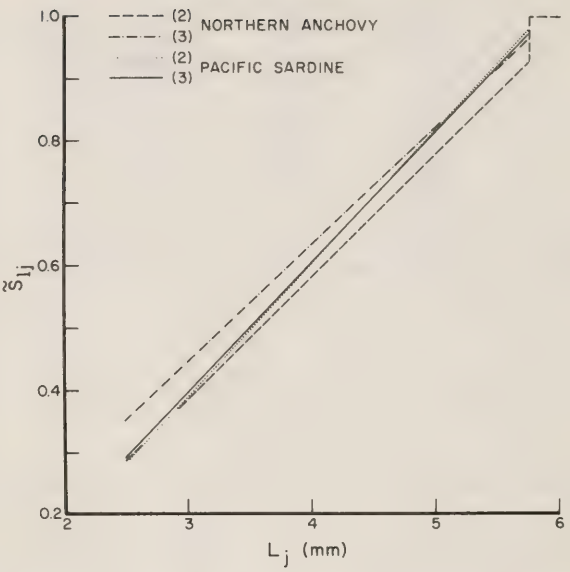

FIGURE 2.—Estimates of mesh retention by type 1 (0.55-mm mesh) net (s_{1j}) against standard length (L_j) for larvae of northern anchovy and Pacific sardine using equations (2) and (3).

where $1-P_{io}$ = portion of larvae of species o not sampled by type i net because of passage through meshes.

Equation (6) implies that an equal number of night and day samples are taken. This is approximately correct. The estimate of P_{1o} for anchovy is 0.60. The estimate of P_{1o} for sardine is 0.67. Thus anchovy larvae are undersampled by about 12% relative to sardine larvae because of differences in mesh retention and size composition.

CATCH CURVE OF TYPE 3 (0.505-MM MESH) NET

Figure 7 shows the catch curve plotted on a semilogarithmic scale of anchovy larvae caught by the type 3 net during 1969 by the CalCOFI. This data is preliminary (P. E. Smith, personal communication) and catches have not been separated by day and night. The interesting feature of this curve is that it is essentially linear

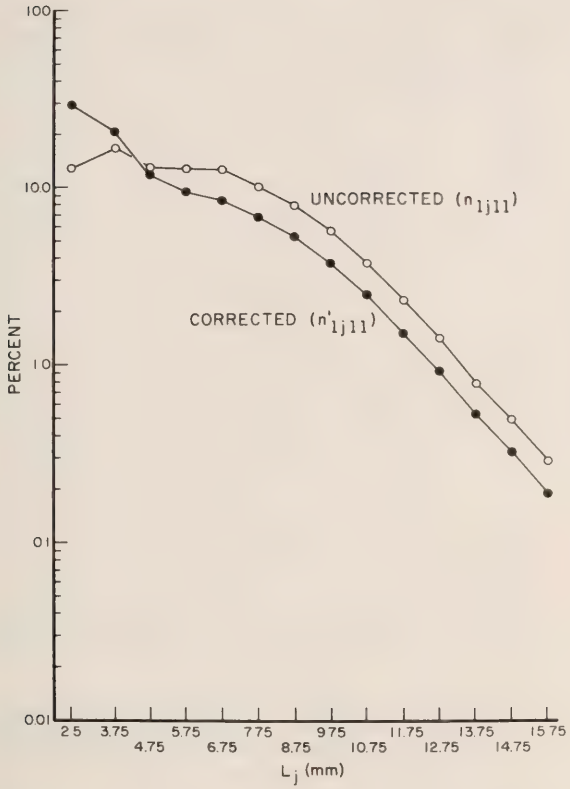

FIGURE 3.—Corrected (n'_{1j11}) and uncorrected (n_{1j11}) catches by standard length (L_j) of northern anchovy taken at night with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

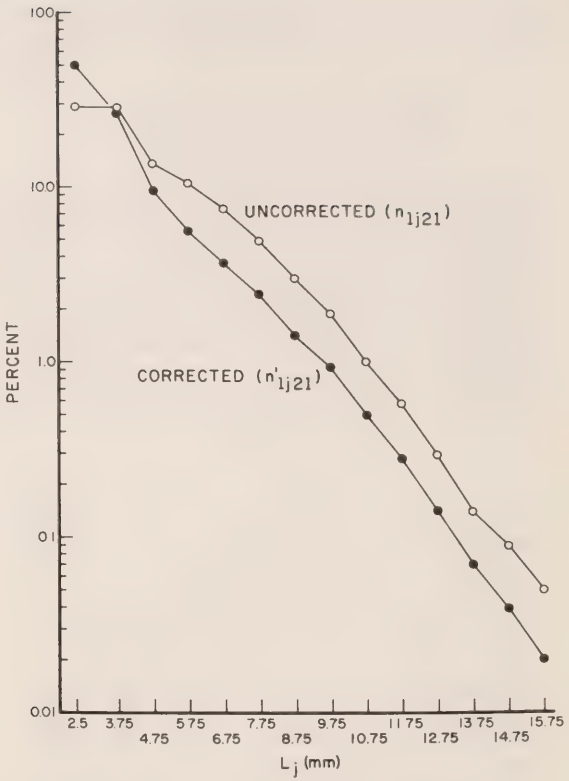

FIGURE 4.—Corrected (n'_{1j21}) and uncorrected (n_{1j21}) catches by standard length (L_j) of northern anchovy taken during day with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

with size. This indicates that few if any small anchovy larvae escape capture by passing through the meshes. Thus a 10% decrease in mesh size and a large decrease in the variance of mesh size changed P_{i1} from 0.60 to about 1. The difference in P_{i1} between the type 1 and type 3 nets means that total catches of anchovy larvae by the type 1 net should be multiplied by 1.7 to be comparable to catches of anchovy larvae by the type 3 net.

DISCUSSION

The similarity of the catch curves of anchovy larvae caught by the type 3 net and the corrected catch curve for the type 1 net suggests that the estimates of s_{1j} are reasonably accurate. It would be a remarkable coincidence otherwise as the data are independent.

It is interesting that the type 3 (0.505-mm mesh width) net apparently retains most if not all anchovy larvae, for the body depth at the insertion of the pectoral fin of 3.75-mm anchovy larvae is about 0.35 mm (P. E. Smith, personal communication) which is considerably less than the mesh width. Smith, Counts, and Clutter (1968) summarized the results of Saville (1958) by concluding that an organism must be wider than the mesh diagonal to be completely retained. A conclusion of this study is that the "diagonal rule" is too conservative for slowly towed nylon nets. Heron (1968) concluded that mesh variability is a very important factor in-

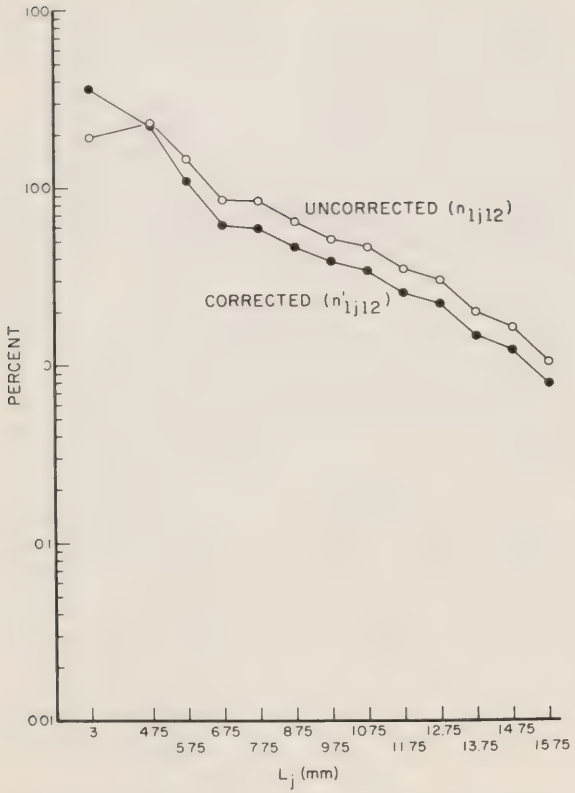

FIGURE 5.—Corrected (n'_{1j12}) and uncorrected (n_{1j12}) catches by standard length (L_j) of Pacific sardine taken at night with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

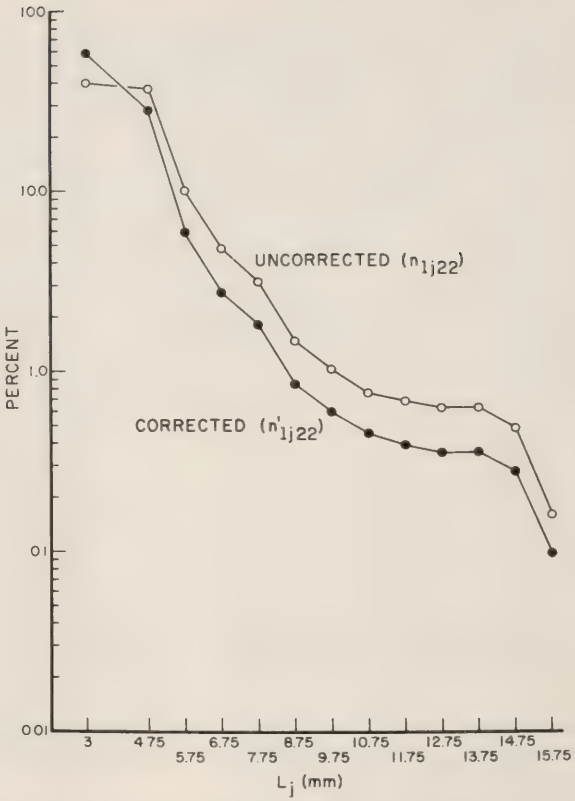

FIGURE 6.—Corrected (n'_{1j22}) and uncorrected (n_{1j22}) catches by standard length (L_j) of northern anchovy taken during day with type 1 (0.55-mm mesh) net. Catches are expressed in percent of total.

fluencing escapement and implied that the coefficient of variation of mesh width is greater for silk than nylon nets. The results of this study agree with Heron's conclusions.

The results indicate that two similar types of sampling gear have greatly different mesh retention properties for anchovy larvae. This implies that considerable care should be taken in the selection of sampling gear if quantitative estimates of the abundance of fish larvae are desired. The similarity in mesh retention shown for anchovy and sardine larvae may be due to the fact that the larval forms are very similar. However the diversity of forms found in fish larvae is tremendous. Mesh retention should be estimated before quantitative estimates of the relative abundance of larvae of different species of fish are attempted. The results indicate that adequate estimates of mesh retention can be made from less than 30 samples containing the desired species of fish larvae. If the mesh retention curve is curvilinear in the region of fish larvae of minimum size, more samples may be necessary.

The reasoning of Hjort (1926) in expecting a critical period in the early life of fish larvae is intuitively pleasing. Hunter (1972) showed experimentally that a much higher density of food organisms is necessary for survival of 4- to 6-mm anchovy than for larger larvae. However, there is no indication of a critical period at the 4- to 6-mm sizes in this study, i.e., there are no major

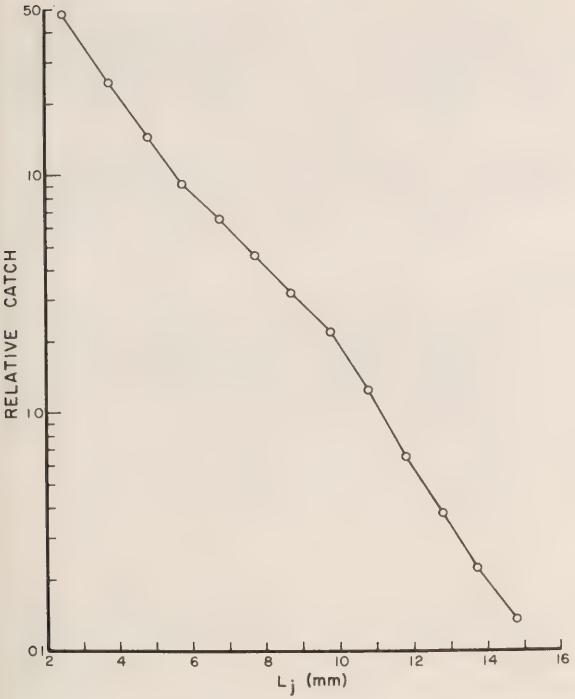

FIGURE 7.—Catches of northern anchovy by standard length (L_j) taken by type 3 (0.505-mm mesh) net.

changes in the slopes of the catch curves. However, since the catches are plotted with size rather than age, a faster rate of growth at small sizes relative to large sizes could cause small size larvae to be relatively undersampled. If this were the case, a critical period could occur but not be indicated by catches plotted with size. Kramer and Zweifel (1970) indicated that the growth rate of anchovy larvae increases rather than decreases with size during the first few millimeters of growth. Another factor that could influence the catch rate of larvae differently with size is avoidance of the net. However, experience indicates that avoidance increases with size (Lenarz, in press). Thus, the large larvae should be relatively undersampled. I conclude, therefore, that available data does not provide any evidence of the critical period for sardine or anchovy larvae. This conclusion is in agreement with other authors that have examined catch curves of fish larvae, e.g., Marr (1956).

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THE INCREASE IN SPAWNING BIOMASS OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

PAUL E. SMITH[1]

ABSTRACT

The northern anchovy, *Engraulis mordax*, is a common fish off the west coast of North America. Its biomass has increased markedly since 1951. The various methods of deriving anchovy spawner biomass from the sardine spawner biomass and analogous census estimates of sardine and anchovy larvae are reviewed. A new compilation of anchovy and sardine larval data is presented for 1940, 1941, 1949, 1950, and 1951-69. The effect of several errors of estimate are examined and it is concluded that none is important enough to affect measurably the trend of increase between 1951 and 1966. Lastly, a current interpretation of the larval survey data is used to estimate the spawning biomass of both sardine and anchovy.

The northern anchovy (*Engraulis mordax* Girard) is a common pelagic schooling fish off the west coast of North America between British Columbia and Baja California (lat 53°N to 22°N). The fishery for northern anchovy has usually been small relative to the Pacific sardine (*Sardinops caerulea* (Girard)) off California but the anchovy catch has been increasing since the late 1930's (Figure 1). Following the collapse of the sardine fishery in the early 1950's, the catch of anchovy exceeded that of sardine. The further decline of sardine catch and the eventual moratorium on sardine, combined with a limited reduction fishery on anchovy, have again allowed the anchovy fishery to exceed that of sardine since the mid-1960's (Messersmith and Associates, 1969).

Routine planktonic larva sampling since 1951 shows an increase in the number of anchovy larvae (Murphy, 1966; Ahlstrom, 1966, 1968) and the present consensus estimate of the spawning population of northern anchovy is about 5 million tons for 1966, the last year for which complete data are available. The same sample data for the Pacific sardine now indicate an extremely small number of larvae and the spawning biomass of the northern subpopulation of the sardine may now be less than 5,000 tons. All anchovy biomass estimates must now be referred to analogous sardine biomass estimates based on the sardine fishery and on sardine and anchovy egg and larva surveys because no fishery-based estimate of anchovy biomass has yet been made: this becomes increasingly difficult and imprecise as the sardine "reference" population diminishes.

The purposes of this paper are to:

1) review the estimates of spawner biomass of the anchovy;
2) present a summary of the incidence of larval anchovy by region and season since 1951;
3) examine the effects of three spawning behavior models on the estimates of spawning biomass;
4) establish a standard reference period for the determination of anchovy biomass without further consideration of the current size of the sardine population.

PREVIOUS ESTIMATES OF ANCHOVY BIOMASS

Messersmith and Associates (1969, p. 9) tabulated all the estimates of anchovy spawning biomass for the years 1940-66. Ahlstrom (MRC,

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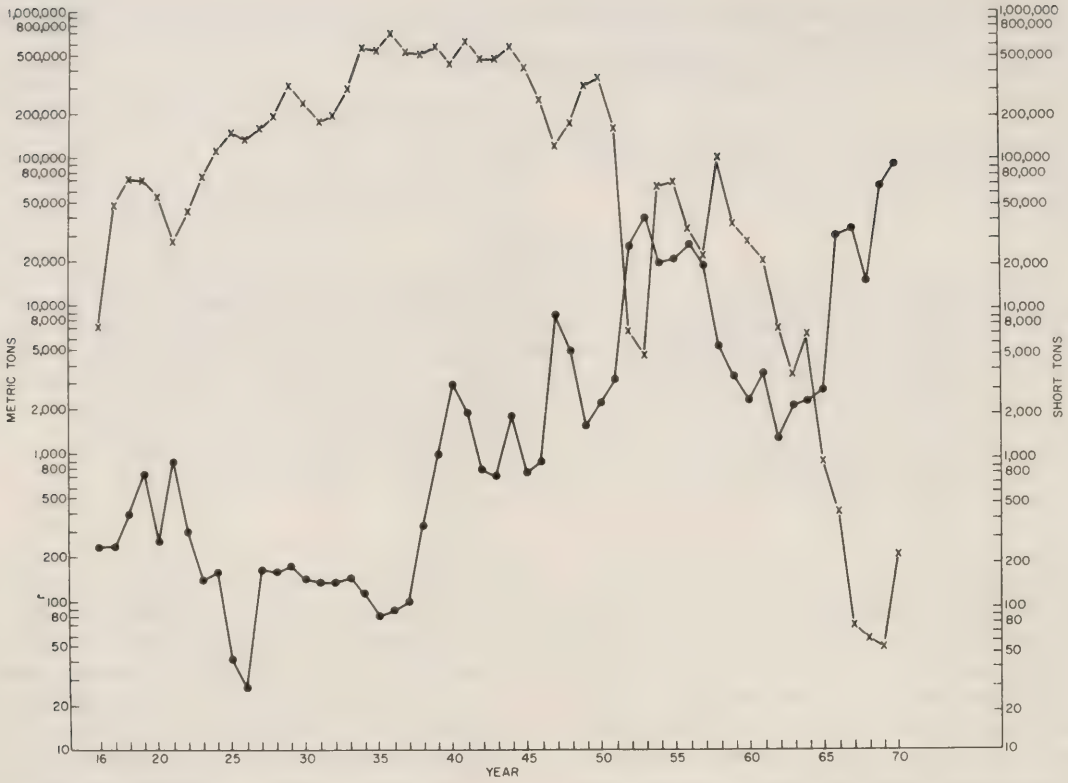

FIGURE 1.—The annual catch of sardine (crosses) and anchovy (solid circles) in the California Current system since 1916. Whole fish reduction was essentially banned in 1919 and a limited whole fish reduction fishery was opened in 1965.

1964)[2] in an informal statement, emphasized the changing ratio of anchovy larvae to sardine larvae from 3.1 to 1 in 1951 to 46.8 to 1 in 1959. In a similarly informal statement, MacGregor (MRC, 1964) described a method for estimating the spawning biomass of pelagic spawning species. That portion of his statement which is related to sardine and anchovy follows:

> Egg and larval surveys conducted over the years have given us a basis for estimating the total numbers of eggs and larvae produced each year in the CalCOFI (California Cooperative Oceanic Fisheries Investigations) survey area for a number of fish species. We also have information on the fecundity of a number of these species and from the combined data can estimate the biomass of spawning adult fish on each species. The number of eggs a fish will produce at one spawning appears to be directly related to the weight of the fish. Thus, we can compute the numbers of eggs produced in one spawning by a ton of female fish as follows:

Species	Millions of eggs
Anchovy	525
. . . .	. .
Sardine	241
. . . .	. .

The above figures represent female fish only. If we assume, as evidence indicates, that for each ton of adult females there is also present a ton of adult males, we would have to divide the number of eggs produced

[2] A review of estimates and procedures was conducted for the California Marine Research Committee (MRC) in 1964 and the texts of the presentations are to be found there. Statements and calculations were neither edited nor formally derived. Quotations from the Appendix to these minutes will be regarded as informal and cited (MRC, date).

by 2 to obtain the number of eggs produced [in one spawning][3] by one ton of adult fish. If we further assume that . . . . about half the [adult] sardine population spawns twice [a year] (average 1½ times) and the anchovy [adult] population spawns 2 or 3 times a year (average 2½ times), we would also multiply millions of eggs by 1½ for the sardine and 2½ for the anchovy. On the above basis the total number of eggs produced by one ton of adult fish of both sexes in one year would be as follows for each species:

Species	Millions of eggs
Anchovy	656
. . . .	. .
Sardine	181
. . . .	. .

It may be seen from the above that, although numbers of eggs or larvae in the plankton may be used as an index of adult abundance, a sardine egg in the plankton represents 3½ times . . . as much adult biomass as an anchovy egg. Estimates of the average biomass of each . . . species for the 3-year period 1955-57 and the average commercial landings for the same period are as follows:

Species	Biomass (tons)	Catch (tons)
Anchovy*	750,000	29,686
. . . . .	. . . . .	. . . .
Sardine	254,000	51,508

* Anchovy larvae caught were used as an estimate of eggs. This may have resulted in underestimation by a factor of 2. Application of this factor brings this biomass of anchovies into line with the material in Murphy's (MRC, 1964) estimate of the anchovy harvest . . . .

[3] In brackets added for clarification.

In another informal statement Radovich (MRC, 1965) cited the change in anchovy to sardine larval ratios (Ahlstrom, MRC, 1964) and stated ". . . in this 8-year period the anchovy maintained its population level fifteen times better than the sardine . . . ." He further pointed out that the necessary ratio of annual survival rates to attain this was 1.4. Should this difference in survival be in the larval stage, the MacGregor (MRC, 1964) biomass estimate should be divided by 1.4 or roughly 1.5, resulting in an estimate of about 1 million tons.

Murphy (MRC, 1964) used an anchovy spawner biomass estimate which was essentially double MacGregor's (MRC, 1964) because he believed that the escapement of anchovy larvae through the mesh of the standard CalCOFI silk net exceeded the escapement of the sardine larvae enough to cancel the effect of anchovy fecundity exceeding sardine fecundity. Thus Murphy's calculation (1966, p. 60) of anchovy spawner biomass for the period 1955-57 was 3.3 million short tons as compared to MacGregor's 1.5 million short tons and Radovich's 1.0 million short tons for the same 3-year period. An estimate by Murphy's method for 1958 would be 5.1 million short tons.

Ahlstrom (1968) estimated that the 1958 anchovy biomass was between 1.80 and 2.25 million short tons and observed further that the biomass had reached a plateau of 4.5 to 5.625 million short tons in the mid-1960's.

TABLE 1.—Comparison of data used for estimating the spawning biomass of northern anchovy.

	Standard haul summation[1]		Summation of average quarterly estimates[2]		Larval census estimates[3]		Standard haul summations[4]	
	Anchovy	Sardine	Anchovy	Sardine	Anchovy	Sardine	Anchovy	Sardine
1951	29,551	11,068	9,826	3,689	15,101	5,774	29,552	11,066
1952	59,626	19,179	20,581	6,437	17,071	5,466	63,057	24,559
1953	99,160	14,400	34,314	4,924	23,680	4,020	103,928	15,055
1954	161,241	26,914	56,665	9,364	38,415	7,297	161,254	26,914
1955	140,183	14,121	51,096	5,554	37,658	4,341	140,188	14,121
1956	134,931	15,523	51,438	5,179	38,508	3,895	134,931	15,523
1957	146,631	9,833	53,921	3,415	40,441	2,432	146,631	9,833
1958	205,733	11,427	75,120	3,845	56,928	2,831	205,457	11,423
1959	206,753	5,374	72,732	2,072	54,168	1,159	206,000	5,308
1960	289,860	8,012	97,602	3,099				
1961	97,103*	1,708*	97,103	1,708				
1962	212,675*	2,258*	212,675	2,258				
1963	205,838*	1,349*	205,838	1,349				
1964	166,517*	2,757*	166,517	2,757				
1965	258,781*	3,573*	258,781	3,603				
1966	380,420	5,640	161,333	2,211				

[1] Ahlstrom 1966, tables 2 and 4 (1965, 1966, numbers from current unpublished data).
[2] Ahlstrom, 1966, 1968.
[3] Ahlstrom, 1968.
[4] Murphy, 1966.
* Quarterly cruises rather than monthly.

TABLE 2.—Stations and pooled areas within each region as used in this study.

Regional name	Pooled areas	Stations
Central California Inshore	6.5	60.52
18 stations	5,270 miles²	60.55
4 pooled areas		63.52
19,970 miles²		63.55
		67.50
		67.55
	6.6	60.60
	4,800 miles²	63.60
		67.60
	7.5	70.52 (51)
	5,100 miles²	70.55 (53)
		73.51 (50)
		73.55 (53)
		77.50 (51)
		77.55
	7.6	70.60
	4,800 miles²	73.60
		77.60
Central California offshore	6.7	60.70
6 stations	6.8	60.80
6 pooled areas	6.9	60.90
28,800 miles²	7.7	70.70
	7.8	70.80
	7.9	70.90
Southern California inshore	8.4	82.47
19 stations	4,589 miles²	83.40
3 pooled areas		83.43
15,348 miles²		87.35
		87.40
		87.45
	9.3	90.28
	5,989 miles²	90.30 (32)
		90.37
		93.27 (28)
		93.30
		97.30
		97.32
		97.35
	9.4	90.45
	4,770 miles²	93.40
		93.45
		97.40
		97.45
Southern California offshore	8.5	80.51 (52)
18 stations	4,747 miles²	80.55
4 pooled areas		83.51
19,147 miles²		83.55
		87.50
		87.55
	8.6	80.60
	4,800 miles²	83.60
		87.60
	9.5	90.50
	4,800 miles²	90.55 (53)
		93.50
		93.55
		97.50
		97.55
	9.6	90.60
	4,800 miles²	93.60
		97.60
Southern California seaward	8.7	80.70
18 stations		83.70
6 pooled areas		87.70
28,800 miles²	8.8	80.80
		83.80
		87.80
	8.9	80.90
		83.90
		87.90
	9.7	90.70
		93.70
		97.70
	9.8	90.80
		93.80
		97.80
	9.9	90.90
		93.90
		97.90
Baja California inshore	10.3	100.29
29 stations	5,535 miles²	100.30
4 pooled areas		100.35
21,089 miles²		103.30
		103.35
		107.32
		107.35
	10.4	100.40
	4,800 miles²	103.40
		103.45
		107.40
	11.3	110.33 (32)
	5,956 miles²	110.35
		113.30
		113.35
		117.26
		117.30
		117.35
		118.39
		119.33
		120.25
		120.30
		120.35
	11.4	110.40
	4,798 miles²	110.45
		113.40
		113.45
		117.40
		117.45
Baja California offshore	10.5	100.50
15 stations	4,800 miles²	103.50
4 pooled areas		107.50
19,200 miles²	10.6	100.60
	4,800 miles²	103.60
		107.60
	11.5	110.50
	4,800 miles²	110.55
		113.50
		113.55
		117.50
		117.55
	11.6	110.60
	4,800 miles²	113.60
		117.60
Baja California seaward	10.7	100.70
19 stations	4,800 miles²	103.70
6 pooled areas		107.70
28,800 miles²	10.8	100.80
	4,800 miles²	103.80
		107.80
	10.9	100.90
	4,800 miles²	103.90
		107.90
	11.7	110.70

TABLE 2.—Continued.

Regional name	Pooled areas	Stations
	4,800 miles²	113.70
		117.70
		117.75
	11.8	110.80
	4,800 miles²	113.80
		117.80
	11.9	110.90
	4,800 miles²	113.90
		117.90
South Baja inshore	12.3	123.37
22 stations	4,459 miles²	127.34
5 pooled areas	12.4	120.40
22,790 miles²	4,800 miles²	120.45
		123.42
		123.45
		127.40
		127.45
	13.2	133.25
	3,931 miles²	137.23
	13.3	130.30
	4,800 miles²	130.35
		133.30
		133.35
		137.30
		137.35
	13.4	130.40
	4,800 miles²	130.45
		133.40
		133.45
		137.40
		137.45
South Baja offshore	12.5	120.50
16 stations	4,800 miles²	120.55
4 pooled areas		123.50
19,200 miles²		123.55
		127.50
		127.55
	12.6	120.60
	4,800 miles²	123.60
		127.60
	13.5	130.50
	4,800 miles²	130.55
		133.50
		137.50
	13.6	130.60
	4,800 miles²	133.60
		137.60
South Baja seaward	12.7	120.70
3 stations	12.8	120.80
3 pooled areas	12.9	120.90
14,400 miles²		

Murphy (1966) estimated the biomass of the spawning stocks of sardine from 1932 to 1959. He also compared the anchovy:sardine larval ratio from 1951 to 1959 and graphically compared this with the larval ratio over a portion (about 20%) of their joint range in 1940 and 1941 (p. 65). The striking decline of the sardine, and the increase of the anchovy biomass, has stimulated speculation on the biological interactions of these species and the MRC (Marine Research Committee of California) has a standing recommendation that 200,000 tons of anchovies and 10,000 tons of sardines be harvested in an experimental attempt to foster the recovery of sardines. It is the primary goal of this recommendation to restore and maintain the balance of sardines and anchovies in the California Current system by manipulation of fishing effort.

The estimates of spawning biomass of the northern anchovy have been based on the spawning biomass of the Pacific sardine as derived from the fishery (Murphy, 1966; Ahlstrom, 1968) and on the assumed relationship between sardine and anchovy fecundity, survival, and escapement of larvae through the meshes of the CalCOFI standard silk survey net (Lenarz, 1972). For convenience, the larva data for all estimates to date are listed in Table 1. A series of stations off southern California was occupied in 1940 and 1941, and the anchovy:sardine ratios were 1.18 (13,962 anchovy to 11,862 sardines) and 1.66 (12,560 anchovy to 7,564 sardines) respectively. The 1940, 1941, 1949, and 1950 data will be referred to later in a section on interaction of sardine and anchovy.

METHOD OF DATA ASSEMBLY

The method of assembling the estimates of larval abundance for this paper differs from that of Sette and Ahlstrom (1948) and Ahlstrom (1954, 1966, 1967, 1968). Two methods of assembly were used previously: the "census estimate" and the "standard haul summation." In the "census estimate" each larva sample count was weighted by the area of a polygon formed by construction of "perpendicular bisectors of lines drawn from the station to each of all surrounding stations" (Sette and Ahlstrom, 1948, p. 521; Ahlstrom, 1968).

$$C_k = 10\sum_{j=1}^{n}\left[\sum_{i=1}^{m} A_s\left(a_i^{-2}\, b_i^{-1}\, c_i\, d_i\right)\right]_j \qquad (1)$$

FIGURE 2.—The selected stations of the CalCOFI grid (see Tables 2 and 3) and the regional boundaries defined for this paper. Columns of stations are indicated .30, .40 . . . .90, and rows of lines are indicated 60, 70, . . . 130. The first two letters of each three-letter group stand for coastal bands, i.e., central California (CC), Southern California (SC), Baja California (BC), South Baja (SB) while the last letter of the three stands for offshore zones roughly parallel to the coast, inshore (0-80 miles from the coast, "I", offshore (80-160 miles from the coast, "O"), and seaward (160-280 miles from the coast, "S"), so that the three letters SCI stand for the southern California inshore region.

TABLE 3.—Description of CalCOFI regions used in this analysis.

Regional name	Stations	Pooled areas	Square miles	Area factor
Central California inshore	18	4	19,970	6.85×10^9
Central California offshore	6	6	28,800	9.88
Southern California inshore	19	3	15,348	5.26
Southern California offshore	18	4	19,147	6.57
Southern California seaward	18	6	28,800	9.88
Baja California inshore	29	4	21,089	7.23
Baja California offshore	15	4	19,200	6.58
Baja California seaward	19	6	28,800	9.88
South Baja inshore	22	5	22,790	7.82
South Baja offshore	16	4	19,200	6.58
South Baja seaward	3	3	14,400	4.94
Totals	183	49	237,544	81.48

TABLE 4.—Equivalent station list off southern California for 1940, 1941, and 1950-72.

Southern California inshore			Southern California offshore		
Station no. used in 1940	Station no. used in 1941	Nearest present station no.	Station no. used in 1940	Station no. used in 1941	Nearest present station no.
02	12	82.47	04	15	80.51
01	11	83.40	05	16	80.55
08	23	83.43	03	13	83.51
10	21	87.35	13	14	83.55
17	22	87.40	24	24	87.50
11	34	87.45	12	25	87.55
21	30	90.28	06	28	80.60
19	31	90.30	09	27	83.60
20	32	90.37	18	26	87.60
22	41	93.27	23	35	90.50
28	51	90.30	31	36	90.55
--	60	97.30	39	45	93.50
35	61	97.32	40	46	93.55
36	62	97.35	41	64	97.50
30	33	90.45	14	55	97.55
29	52	93.40	32	37	90.60
34	54	93.45	25	47	93.60
37	63	97.40	33	--	97.60
38	53	97.45			

where A_s = area of a polygon constructed of perpendicular bisectors of lines between station "i" and all adjacent stations expressed as number of 10 m^2 areas

C_{kf} = estimate of abundance of larvae in year "k" and "f" takes the value of the number of the equation

C_i = number of larvae in "ith" sample

a_i = area of mouth of the net used at the "ith" station

b_i = length of tow in meters estimated from a calibrated flow meter at station "i"

d_i = tow depth in meters estimated from the wire angle at maximum wire out at station "i"

m = number of stations

n = number of monthly cruises.

In the "standard haul summation" approach the sums of all tows on regularly occupied stations for each monthly cruise were totaled for the year without weighting for represented area.

$$C_k = 10 \sum_{j=1}^{n} \left[\sum_{i=1}^{m} \left(a_i^{-2}\ b_i^{-1}\ c_i\ d_i \right) \right]_j . \quad (2)$$

To accommodate the quarterly cruises Ahlstrom (1966, 1968) established a modification of this in which the quarterly averages of 1 to 3 monthly cruise summations were added to make an

annual total (Ahlstrom, 1966, Table 8; 1968, Table 3).

$$C_k = 10 \sum_{q=1}^{4} \left\{ \sum_{j=1}^{n} \left[\sum_{i=1}^{m} \times \left(a_i^{-2}\ b_i^{-1}\ c_i\ d_i \right) \right]_j n^{-1} \right\}_q . \quad (3)$$

Murphy (1966) used the monthly version of Ahlstrom's standard haul summation (Table 1).

The method used here is called the "regional census estimate"

$$C_{k4} = 10\, A_r m^{-1} \left[\sum_{i=1}^{m} \left(a_i^{-2}\ b_i^{-1}\ c_i\ d_i \right) \right] \quad (4)$$

where C_{k4} = estimate of abundance of larvae in region "r" in each quarter

A_r = Area of region "r" in numbers of 10 m^2 areas.

This method of assembly combines the simplicity of the "standard haul summation" and the areal weighting of the previously used census estimates. The regional census estimate consists of the mean number of larvae per standard area (10 m^2 sea surface) of all stations taken within a region for a quarter of the year times the number of standard areas within the region. The same 183 stations or nearby alternates were used within the routinely occupied area as defined by Smith, Ahlstrom, and Casey (1970, Figure 1). The selected stations and acceptable alternates are listed in Table 2 and the regions are illustrated in Figure 2 and defined by area and area factor in Table 3.

The 1940 and 1941 stations have been assigned to the two southern California regions (Table 4) in which these cruises were conducted. The number of stations per unit area has been held nearly constant by the elimination of excess stations in the early cruises. The 1949 station equivalents are listed in Table 5. From 1950 to 1972 stations have been standard in placement.

TABLE 5.—Equivalent station list for the CalCOFI survey pattern for 1949 and 1950-72.

Area	Station no. used in 1949	Nearest present station no.
Central California inshore	601	63.58
	701	72.56
Central California offshore	602	62.68
	603	61.78
	604	61.87
	702	71.66
	703	71.76
	704	71.85
Southern California inshore	901	92.39
Southern California offshore	801	82.57
	902	92.48
	903	92.58
Southern California seaward	802	82.67
	803	82.77
	804	82.87
	904	92.68
	905	92.78
Baja California inshore	1001	101.34
	1002	101.44
	1101	111.38
	1102	111.48
Baja California offshore	1003	102.54
	1004	102.64
	1103	111.58
Baja California seaward	1005	102.74
	1006	102.84
	1007	102.94
	1104	111.68
	1105	112.78
	1106	112.88
	1107	112.98
Southern Baja inshore	1201	122.44
Southern Baja Offshore	1202	122.53
Southern Baja seaward	1203	123.63
	1204	123.73
	1205	124.83

Extra cruises, additional lines, and stations on lines have been added periodically, resulting in some increase in station density in some areas. To stabilize sampling effort and remove possible effects of added effort nearshore, all but 183 stations and their nearby equivalents have been eliminated from further consideration for the 16-year compilation of regional census estimates. The number of stations eliminated each year are summarized in Table 6.

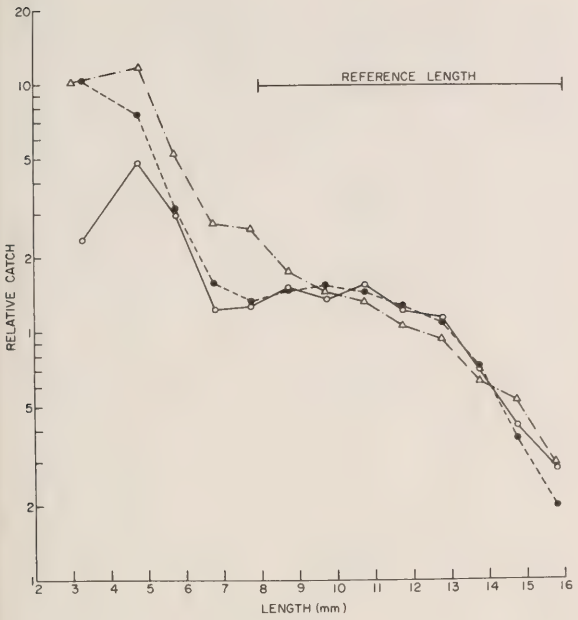

FIGURE 3.—The size frequency of sardine larvae caught in the CalCOFI standard silk net (0.55 mm). The triangle dot-dash curve represents the 1951-60 catch from the selected stations in all eleven regions; the black dot-dash curve represents the 1940 catch from selected stations in the southern California inshore and offshore region and the clear dot solid line represents the 1941 catch from the same two regions. Relative catch refers to the catch at a standard size group (3.00, 3.25 (1940-41), 4.75, 5.75 ... 15.75 mm), divided by the average catch from size groups 8.75 to 15.75.

ESCAPEMENT AND AVOIDANCE BY ANCHOVY AND SARDINE LARVAE

The chief errors causing underestimates of C for both anchovy and sardine larvae are those attributable to larvae "escaping" through the meshes of the standard plankton net (see Lenarz, 1972, p. 839) and larvae "avoiding" the mouth of the net (Silliman, 1943; Ahlstrom, 1954, 1959; Clutter and Anraku, 1968). While "escapement" and "avoidance" are important biases to consider in the study of larva growth and mortality, I consider them beyond the scope of this paper. The estimate of anchovy biomass is based on a relative estimate of the number of anchovy larvae and sardine larvae. I must treat escapement and avoidance briefly, since they act differently on the anchovy and sardine and vary from season to season and with changes in sampling gear.

Lenarz (1972) found no appreciable difference in size-specific escapement of sardine and anchovy through net apertures. However, newly hatched anchovy larvae are considerably smaller than sardine larvae. This leads to a variation in the degree of bias (Murphy, 1966) to such escapement. In Figure 3 the catch of all standard sizes of sardine is related to the average catch between 8.75 and 15.75 mm, a size range I assume to be completely retained on 0.55-mm mesh width silk. The primary line is the average size composition for the period 1951-60 for the sardine. The size composition of the 1940

TABLE 6.—Stations eliminated from data assembly for regional census estimates.

Year	No. of stations occupied	183 stations reported each cruise	Stations not reported	Percent reported
1951	1,436	1,026	410	71.4
1952	1,376	1,167	209	84.8
1953	1,346	1,137	209	84.5
1954	1,473	1,217	256	82.6
1955	1,425	1,121	304	78.7
1956	1,399	1,129	270	80.7
1957	1,493	1,165	328	78.0
1958	1,851	1,276	575	68.9
1959	2,182	1,574	608	72.1
1960	1,810	1,305	505	72.1
1961	953	699	254	73.3
1962	920	659	261	71.6
1963	881	659	222	74.8
1964	877	680	197	77.5
1965	1,099	658	441	59.9
1966	1,979	1,487	492	75.1

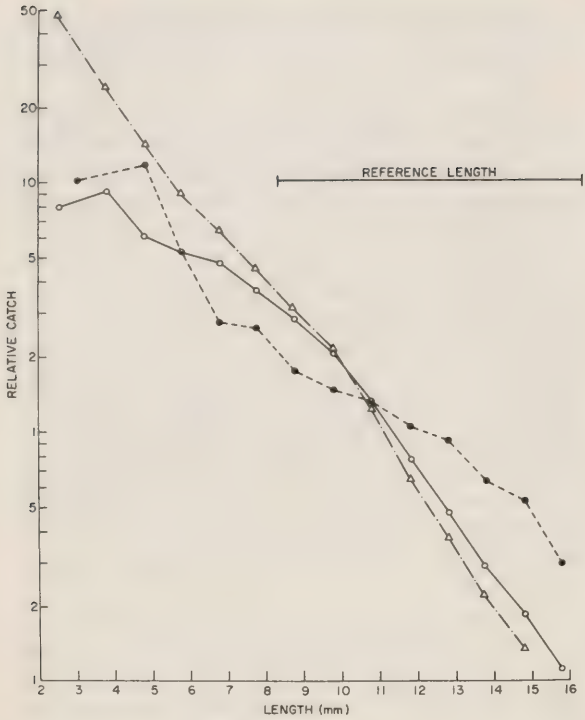

FIGURE 4.—The size frequency of sardine and anchovy larvae. The black dot-dash line is sardine larvae caught in the standard CalCOFI silk net between 1951 and 1960 in all regions from January to June inclusive. The clear dot solid line is anchovy larvae caught in the standard CalCOFI silk net between 1951 and 1960, in all regions from January to June inclusive. The triangle dot-dash line is anchovy larvae caught in the new CalCOFI nylon net (0.505-mm nylon rather than 0.55-mm silk) from January to June 1969 in all regions.

and 1941 sardine catches are included for later reference. In Figure 4, the 1951-60 size composition of sardine is compared to the anchovy for the same period. Anchovy retention in a new net with smaller, more regular meshes (0.505-mm nylon) and more mesh area is included for comparison. All samples reported in the size frequency graphs are from the first half of the year to facilitate comparison with earlier samples and eliminate the effects of poor sampling coverage in the latter half of the year.

Ahlstrom (1954) acknowledged that larger larvae may avoid capture at night as in the daytime. Avoidance is more pronounced in the daylight. In the sardine the night-to-day ratio of catches increases 0.6971 per mm of growth after 4.75 mm (Ahlstrom, 1954, p. 129). Similarly, the anchovy night-to-day catch ratio increases 0.64 for each millimeter growth after 3.5 mm (Ahlstrom, 1959, p. 136). Lenarz (in press) described the annual and diurnal variation in size specific catch rate for sardine, anchovy, hake, and jack mackerel. An important source of variability in avoidance bias is a shift of spawning season. For example, length of day varies from 9.6 hr in winter to 14.8 hr in summer at the latitude of San Francisco near the northern boundary of the survey grid and from 10.6 to 13.7 hr off south Baja California at the southern boundary of the sample grid (54% and 29% respectively). For the 10-year period, 1951-60, the ratio of night-caught to day-caught larvae was 1.72 for sardines and 2.45:1 for anchovy. When the average catch per positive tow by month is corrected for day length at San Francisco the anchovy:sardine ratio changes from 2.96:1 to 3.75:1 for the same decade. A proportionate shift of anchovy spawning toward June would for example, accentuate this difference.

The importance of avoidance and escapement

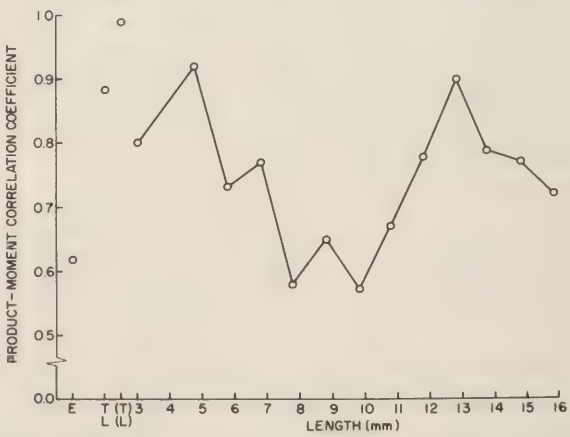

FIGURE 5.—The correlation coefficient between the annual total regional census estimates of sardine eggs and larvae by size class with the Murphy (1966) sardine biomass estimates. The first point is for total eggs, 1951-59; the second point is for total larvae, 1951-59; the third point is for total larvae with 1953 and 1959 censored. The succeeding points are for standard-size classes for all years 1951-59.

TABLE 7.—A comparison of the regional census estimate (A), separately weighted nearshore (B), and 1 month per quarter sampling (C), in the southern California inshore region, 1951-60.

		Winter	Spring	Summer	Fall	Total	Annual rank
1951	A	135	609	111	540	1,395	9
	B	175	879	92	441	1,587	9
	C	289	251	76	276	892	10
1952	A	87	261	314	134	796	10
	B	70	229	336	119	754	10
	C	52	315	531	122	1,020	9
1953	A	578	184	763	1,904	3,429	6
	B	519	139	734	1,409	2,801	6
	C	163	339	1,089	728	2,319	8
1954	A	3,123	516	519	237	4,395	3
	B	1,006	445	412	180	2,043	7
	C	2,577	332	934	149	3,992	5
1955	A	2,012	1,074	849	150	4,085	4
	B	1,682	1,006	737	117	3,542	4
	C	1,941	930	1,111	55	4,037	4
1956	A	236	1,166	708	156	2,266	8
	B	186	1,009	635	117	1,947	8
	C	302	1,632	708	129	2,771	7
1957	A	3,314	3,601	791	267	7,973	1
	B	3,650	3,264	933	238	8,085	1
	C	4,951*	4,060	791	154	9,956	1
1958	A	2,316	2,912	403	63	5,694	2
	B	2,186	3,226	417	36	5,865	2
	C	1,753	4,246	554	51	6,604	2
1959	A	972	2,303	108	101	3,484	5
	B	907	2,530	111	72	3,640	3
	C	413	5,354	218	19	6,004	3
1960	A	1,579	1,448	198	34	3,259	7
	B	1,692	1,564	189	36	3,481	5
	C	263	2,394	296	34	2,987	6

* February
B $r_s = 0.85$
C $r_s = 0.90$

to biomass estimation is solely a function of the variability these biases cause with respect to year-to-year differences between the capture and retention of sardine and anchovy larvae. For example, in Figure 5 the product moment regression coefficients, r for sardine egg or larval census estimate versus sardine biomass are plotted by total eggs, total larvae (1951-59), total larvae with outlyer censored (1953-59), and each larval size interval through 15.75 mm. All the coefficients are high and positive with pronounced minima at the egg stage and at the 9.75 mm stage. One might ascribe the minimum associated with eggs to the effect of "patchy" distribution on precision of estimate. I have no ready explanation of the 9.75 mm minimum or the 12.75 mm maximum which follows it.

Sette and Ahlstrom (1948, p. 521) discussed the concept of "area of station" relative to sardine eggs. Trial calculations of the same kind suggest that with respect to sardine larvae, assigning equal areas to stations is also close to the more exact method of erecting perpendicular bisectors to each nearest station and using the area of the polygon so formed. For anchovy larvae, however, there may be an important problem. To study this problem, the southern California inshore region was divided into "nearshore", i.e., the standard station closest to shore on each line, and "nearshore-excluded" segments. In the 40 quarters of the years 1951-60, the mean concentration of eggs per positive station in the "nearshore" region exceeded that of the "nearshore-excluded" section by 35%. Similarly the

proportion of positive stations was 87% "nearshore" and 68% in the "nearshore-excluded" region with respect to anchovy larvae.

In Table 7 I have compared the annual estimates of anchovy larvae using the quarterly regional census estimate of the entire region with the same estimate using the sum of the nearshore and nearshore-excluded segments of the region. The latter estimate is 8% lower than the regional census estimate, but it is not likely to be a bias since of the 10 annual estimates, the single estimate exceeds the partitioned estimate 5 times while the reverse is true an equal number of times. The Spearman rank coefficient of correlation is 0.85. Also, a comparison of the annual estimates from 1951 to 1959 regional census estimates and those from a census estimate by Ahlstrom (1967, Table 2) shows a Spearman rank correlation coefficient of 1.00. Thus, we may conclude that errors of the kind involving nearshore gradients in the incidence and intensity of anchovy spawning and larval survival, while important for some applications, do not measurably affect the regional census estimates.

One may reasonably ask whether estimates generated from monthly cruises are comparable to larval abundance estimates from a single cruise in each quarter. In Table 7 I have compared the annual estimates of anchovy larvae using all regular occupied stations within the quarter and a similar estimate using only January, April, July, and October, with February used in 1957 because the January cruise was incomplete. The Spearman rank coefficient for the comparison is 0.90: the mean value of the estimates from monthly cruises is 10% below the estimates from one cruise per quarter but in 5 years the monthly derived estimates exceed the quarterly and in 5 years the reverse is true. Thus, I conclude that differences which may arise from comparing estimates from quarterly and monthly cruises are not large enough to affect this study.

Technical errors should be relatively small and affect the catches of sardine and anchovy similarly. For example, the factor a_i, the area of mouth of the net is usually known to within 5%, the factor b_i is modified by the flow through the mouth of the net so that the length of tow is

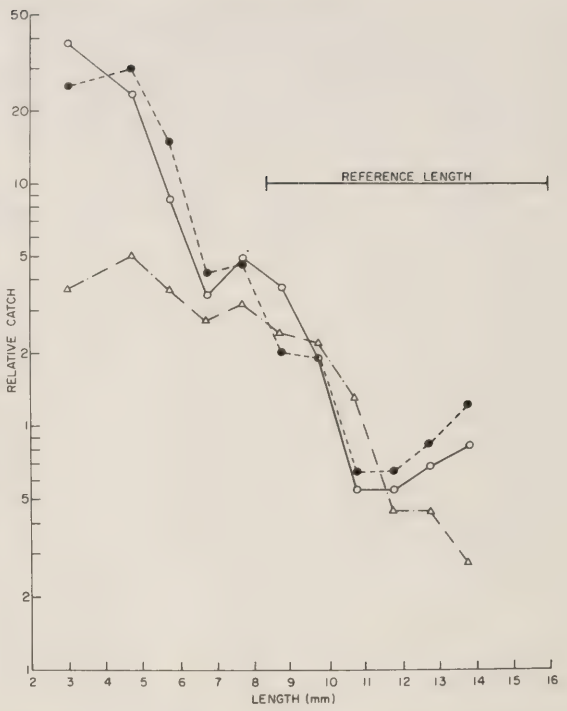

FIGURE 6.—The size frequency of sardine larvae captured in 1951-60 in the southern California inshore (clear dot, solid line), offshore (black dot, small dash), and seaward (triangle, large dash) regions. The size frequency effect is attributed to offshore transport (see text).

underestimated by 13-15%: an error as great as 5-10% results from the flowmeter being centered in the backwash of the bridle apex hardware (Smith and Clutter, 1965; Tranter and Smith, 1968; Mahnken and Jossi, 1967).

Two biases, which have yet to be evaluated, are likely to be important. In cold water, the larvae may tend to grow more slowly. Thus the regional census estimate for a cold quarter or cold year could prolong the period for which the larvae are vulnerable to sampling. Similarly, larvae may persist without food for extended periods yielding the same kind of error mentioned for temperature. No estimate has been made for either bias for anchovy or sardine larvae.

All the sardine and anchovy larvae collected by the CalCOFI net have been subjected to trans-

port with the wind-driven layer of the ocean (Sette, 1943). While the entire problem of transport is beyond the scope of this paper, a comparison of size frequencies of larvae in the southern California inshore, offshore, and seaward regions shows a disproportionately lower number of younger larvae in samples from farther offshore (Figures 6 and 7). The most likely explanation of these data is that older larvae transported to the offshore regions are present in excess of the numbers that have been spawned and hatched there. Further, this implies that the larva size frequency slope in the spawning area is biased for the same reason. If the usual sampling grid encloses the spawning area and the areas to which larvae are transported no overall bias should ensue.

The MacGregor estimate of anchovy and sardine biomass cited above, mentioned specific numbers of spawnings per year and sex ratios. Neither of these has been suitably evaluated as yet. At present, there is no way of calculating the number of batches spawned per year. In this paper, I assume that the anchovy is twice as fecund as sardine. An attempt will be made to evaluate the sensitivity to multiple spawning by proposing three spawning models, below. The sex ratio is presently derived from the fishery which is conducted over a very small proportion of the anchovy range. Since males are somewhat smaller, they may be expected to be recruited to the fishery somewhat later than females. In this report, the simple assumption of equality of biomass will be maintained. This will tend to overestimate the adult biomass by the degree in which the male biomass is overestimated.

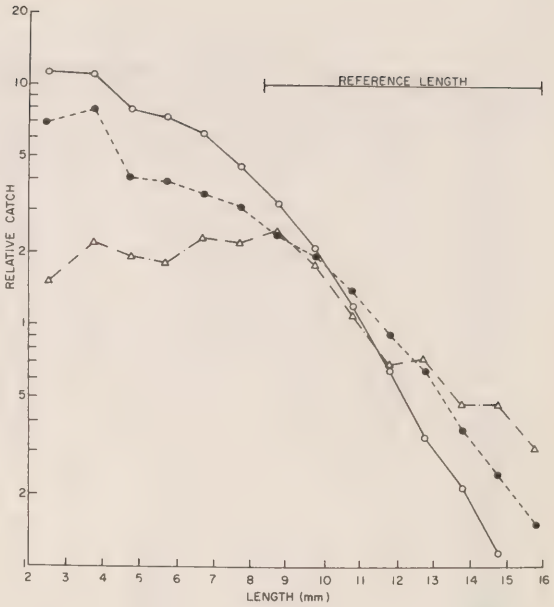

FIGURE 7.—The size frequency of anchovy larvae captured in 1951-60 in the southern California inshore (clear dot, solid line), offshore (black dot, small dash), and seaward (triangle, large dash) regions. The size frequency effect is attributed to offshore transport (see text).

TABLE 8.—Sample size frequency distribution for sardine and anchovy. Total larvae per 10 m² sea surface.

Mid-range x	Sardine f	fx	$fx/\Sigma fx$	Cumulative percent	Anchovy f	fx	$fx/\Sigma fx$	Cumulative percent
0.7	4	2.8	0.000	0.0	4	2.8	0.000	0.0
1.4	51	71.4	0.000	0.1	79	110.6	0.000	0.0
2.8	453	1,268.4	0.009	0.9	886	2,480.8	0.002	0.2
5.6	320	1,792.0	0.012	2.2	707	3,959.2	0.003	0.4
11.2	312	3,494.4	0.024	4.6	814	9,116.8	0.006	1.0
22.4	289	6,473.6	0.045	9.1	789	17,673.6	0.012	2.2
44.7	257	11,487.9	0.079	17.0	752	33,614.4	0.022	4.4
89.1	179	15,948.9	0.110	28.0	725	64,597.5	0.043	8.7
177.8	127	22,580.6	0.156	43.7	618	109,880.4	0.072	15.9
354.8	78	27,674.4	0.191	62.8	579	205,429.2	0.135	29.4
707.9	44	31,147.6	0.216	84.4	369	261,215.1	0.172	46.6
1,412.5	14	19,775.0	0.137	98.0	247	348,887.5	0.230	69.6
2,818.4	1	2,818.4	0.019	100.0	94	264,929.6	0.174	87.1
5,623.4					23	129,338.2	0.085	95.6
11,220.2					4	44,880.8	0.030	98.5
22,387.2					1	22,387.2	0.015	100.0
N	2,129				6,691			
$\bar{X}$	67.88				226.95			
Σfx		144,535.4				1,518,503.7		

TABLE 9.—Regional census estimates of total anchovy larvae (0-: no sampling).

Year	Quarter	Regions[1]											
		CCI	OCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1940	1	0–	0–	771	196	0–	0–	0–	0–	0–	0–	0–	967
	2	0–	0–	258	214	0–	0–	0–	0–	0–	0–	0–	472
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1941	1	0–	0–	184	351	0–	0–	0–	0–	0–	0–	0–	535
	2	0–	0–	422	579	0–	0–	0–	0–	0–	0–	0–	1,001
	3	0–	0–	27	8	0–	0–	0–	0–	0–	0–	0–	35
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1950	1	0	0	10	9	4	43	17	1	13	5	0	102
	2	0	0	232	319	27	115	23	0	152	13	0	881
	3	994	265	338	5	2	9	1	0	2	3	0	1,619
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1951	1	5	0	135	8	0	289	17	150	2,537	147	1	3,289
	2	4	6	609	24	5	203	66	78	289	179	80	1,543
	3	25	53	111	21	0	454	0	0	49	57	0	770
	4	18	0	540	21	0	266	2	0	55	0	0	902
1952	1	0–	0–	87	33	0	1,372	111	0	1,762	40	0	3,405
	2	0	0	261	7	1	732	32	0	1,665	145	0	2,843
	3	7	69	314	16	3	462	1	2	240	12	2	1,128
	4	0	0	134	23	0	558	31	0	8	2	0	756
1953	1	0–	0–	578	67	6	1,649	247	2	4,160	78	227	7,014
	2	0	0	184	17	0	535	85	2	424	238	14	1,499
	3	2	0	763	38	7	373	2	0	150	33	0	1,368
	4	0–	0–	1,904	882	0	831	48	0	84	2	0	3,751
1954	1	654	0–	3,123	723	6	1,090	97	6	4,116	474	615	10,904
	2	1	0	516	98	2	878	28	3	1,872	498	350	4,246
	3	451	0	519	307	426	182	0	0	231	191	0	2,307
	4	58	0–	237	73	11	234	153	0	301	9	0	1,076
1955	1	0–	0–	2,012	283	6	7,152	499	11	750	312	2	11,027
	2	2	0	1,074	246	6	540	266	296	787	380	24	3,621
	3	7	0	849	184	35	257	3	0	602	9	27	1,973
	4	5	10	150	19	0	210	15	0	59	7	4	479
1956	1	0–	0–	236	203	46	1,140	832	409	1,786	1,107	2	5,761
	2	0	0	1,166	63	14	2,239	37	1	1,737	154	2	5,413
	3	247	0	708	562	21	1,413	0	0	807	8	0	3,766
	4	0–	0–	156	115	4	0–	0–	0–	0–	0–	0–	275
1957	1	0–	0–	3,314	1,085	969	2,720	102	3	2,683	69	0	10,945
	2	20	21	3,601	814	69	853	104	8	426	44	13	5,973
	3	5	20	791	592	64	380	1	0	358	234	17	2,462
	4	64	0	267	229	4	86	0	0	10	0	0	660
1958	1	1,620	1,227	2,316	2,407	268	4,680	618	16	4,606	788	5	18,551
	2	252	15	2,912	1,168	497	1,099	384	2	165	57	44	6,590
	3	413	387	403	1,508	84	143	5	0	15	0	0	2,958
	4	11	5	68	34	0	54	2	0	4	0	0	173
1959	1	1,722	0	972	4,452	654	701	51	1	1,595	51	0	10,199
	2	1,101	318	2,303	3,074	498	3,227	651	1	464	453	0	12,090
	3	232	128	108	242	33	82	1	1	197	9	0	1,033
	4	5	0	101	2	0	9	4	0	20	0	0	141
1960	1	185	0	1,579	1,393	279	4,647	1,697	592	6,821	2,327	686	20,206
	2	127	64	1,448	2,694	1,065	2,679	626	259	582	472	11	10,027
	3	155	105	198	70	22	106	69	6	294	7	0	1,032
	4	1	0	34	9	0	67	0	0	21	2	15	149
1961	1	7	0	144	45	0	2,145	143	0	13,436	234	0	16,154
	2	10	0	1,513	955	2,258	2,186	516	215	3,068	1,683	115	12,519
	3	677	310	359	1,127	1,070	114	1	0	27	9	0	3,694
	4	35	15	18	25	4	32	3	2	30	7	0	171
1962	1	56	0	2,285	825	3	2,413	1,021	24	12,570	2,248	0	21,445
	2	877	0	6,555	5,953	5,900	15,483	1,516	228	1,208	1,631	186	39,537
	3	0–	0–	1,214	120	40	505	4	5	162	92	0	2,142
	4	41	5	134	65	8	124	1	0	256	0	0	634

TABLE 9.—Continued.

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1963	1	7	0	7,543	1,481	73	8,088	5,446	688	8,730	381	184	32,621
	2	1,395	175	3,291	6,132	12,821	1,810	389	42	507	182	86	26,830
	3	0—	0—	180	649	133	187	8	8	305	21	7	1,498
	4	0—	0—	279	161	2	92	3	2	45	0	0	584
1964	1	1,420	0	4,137	3,552	7,213	2,895	133	66	6,678	148	5	26,247
	2	3,056	82	4,524	6,223	3,656	1,063	1	0	384	73	77	19,139
	3	538	125	353	1,814	1,516	1,058	26	15	204	6	0	5,655
	4	0—	0—	945	110	3	71	0	2	81	0	0	1,212
1965	1	16	0	10,145	3,803	669	6,158	1,136	1,013	7,171	396	5	30,512
	2	1,160	0	6,870	7,561	6,219	2,257	424	1,112	6,205	91	17	31,916
	3	75	5	6,304	3,130	3,042	1,056	286	4	866	5	0	14,773
	4	0—	0—	1,037	733	121	185	0	0	15	0	0—	2,091
1966	1	2,973	0	7,078	4,285	409	4,426	275	9	3,289	189	15	22,948
	2	181	0	7,823	9,902	1,164	1,065	63	5	1,023	2	0	21,228
	3	738	56	2,427	960	214	881	36	2	454	90	0	5,858
	4	51	2	1,022	62	14	181	4	0	830	0	0	2,166
1967	1	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—
	2	0—	0—	5,646	2,565	367	1,901	59	0	618	23	0	11,179
	3	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0
	4	0—	0—	0—	0—	0—	966	155	8	224	605	0	1,958
1968	1	458	0	3,318	3,259	406	2,342	1,851	0	0—	0—	0—	11,634
	2	4	0	4,020	1,194	697	960	397	0	303	361	0	7,936
	3	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—
	4	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—	0—
1969	1	919	0	16,404	11,163	1,028	5,712	1,671	5	4,198	588	38	41,726
	2	3	0	5,982	2,364	294	3,459	350	196	612	237	3	13,500
	3	28	91	3,101	678	92	282	13	19	178	13	0	4,495

[1] CCI = Central California inshore
CCO = Central California offshore
SCI = Southern California inshore
SCO = Southern California offshore
SCS = Southern California seaward
BCI = Baja California inshore
BCO = Baja California offshore
BCS = Baja California seaward
SBI = South Baja inshore
SBO = South Baja offshore
SBS = South Baja seaward

The anchovy spawns over a small portion of its range apparently while still schooled; it also spawns over a small portion of the day (25%); it now appears that most spawning takes place just after the full moon, ca. 20% of the lunar month (Smith).[4] In addition, the spawning behavior is highly seasonal with most spawning occurring in the first half-year. Biases result from sampling during a period in which spawning is occurring (Sette and Ahlstrom, 1948, p. 520), and similar errors may result from missing or oversampling spawning peak periods or dense small patches. Although patches would tend to disperse toward randomness, this process appears to be very slow relative to the duration of the larval stage. Patchiness persists and may be augmented by predation. For this reason, the samples have been pooled to reduce variance wherever possible. Nevertheless, sample sizes range from zero to tens of thousands of larvae, and a pooled summary may still be based on a chance large sample. In all cases, the above error analysis was done with a sample frequency plot in view and all "outlyers" were examined for effect on the sampling question. All samples taken between 1951 and 1960 are listed by frequency distribution in Table 8 for sardine and anchovy total larvae.

Anchovy larvae abundance (Table 9) and sardine larvae abundance (Table 10) for 11 regions and the years 1940, 1941, 1949-69, are listed for each region and quarter in which sampling took place at standard stations. Figure 8 shows the comparison of the regional census estimates and standard haul summations from 1951 to 1966 (Ahlstrom, 1968). The close agree-

[4] Smith, P. E. Lunar periodicity in the spawning of the northern anchovy (*Engraulis mordax*). Unpublished manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92037.

TABLE 10.—Regional census estimates of total sardine larvae (0-: no sampling).

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1940	1	0–	0–	81	343	0–	0–	0–	0–	0–	0–	0–	424
	2	0–	0–	141	210	0–	0–	0–	0–	0–	0–	0–	351
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1941	1	0–	0–	154	211	0–	0–	0–	0–	0–	0–	0–	365
	2	0–	0–	277	313	0–	0–	0–	0–	0–	0–	0–	590
	3	0–	0–	1	5	0–	0–	0–	0–	0–	0–	0–	6
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1949	1	0	0	0	0	0	9	2	0	0–	20	3	34
	2	0	0	2	11	14	259	1	1	300	2	3	593
	3	304	7	5	12	5	0	0	0	0	0	1	334
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1950	1	0	0	0	0	0	92	1	0	117	128	2	340
	2	0	2	116	206	128	60	91	3	1,951	402	0	2,959
	3	9	4	3	2	2	1	2	0	10	11	0	44
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1951	1	0	0	3	0	0	19	4	0	235	63	0	324
	2	0	0	3	89	18	101	103	8	1,313	107	17	1,759
	3	0	0	4	1	0	270	0	0	94	7	0	376
	4	0	0	0	0	0	146	0	0	79	1	0	226
1952	1	0–	0–	1	5	0	117	90	0	464	87	2	766
	2	0	0	27	51	1	95	194	0	427	731	0	1,526
	3	0	0	8	39	0	49	12	0	168	5	0	281
	4	0	0	0	0	0	37	0	0	19	4	0	60
1953	1	0–	0–	0	0	0	48	199	0	342	94	40	723
	2	0	0	1	0	0	73	509	0	123	370	4	1,080
	3	0	0	1	0	0	86	0	0	100	22	0	209
	4	0–	0–	0	0	0	62	0	0	113	2	0	177
1954	1	0	0–	0	1	0	20	185	93	681	51	110	1,141
	2	1	0	80	320	204	355	63	37	290	140	9	1,499
	3	0	0	4	0	0	59	2	0	166	75	0	306
	4	0	0–	0	0	0	5	0	0	239	3	0	247
1955	1	0–	0–	1	2	8	179	278	285	142	110	0	1,005
	2	0	0	35	146	85	72	99	70	14	8	0	529
	3	0	0	1	31	34	228	4	0	34	9	0	341
	4	0	0	0	0	0	18	0	0	64	2	0	84
1956	1	0–	0–	0	0	0	71	58	33	330	54	0	546
	2	0	0	2	173	48	52	11	14	70	93	0	463
	3	0	0	2	43	9	307	0	0	335	0	0	696
	4	0–	0–	1	0	0	0–	0–	0–	0–	0–	0–	1
1957	1	0–	0–	0	0	0	177	1	2	144	12	0	336
	2	0	0	3	188	4	19	3	1	1	0	0	219
	3	0	20	15	0	0	303	0	0	108	0	0	446
	4	0	0	0	38	0	80	0	0	15	3	0	136
1958	1	0	0	83	52	0	259	0	0	224	21	0	639
	2	3	0	52	27	4	9	2	0	12	1	67	177
	3	0	0	26	94	2	287	1	0	217	0	0	627
	4	0	0	0	0	0	9	0	0	1	0	0	10
1959	1	0	0	74	15	3	24	0	0	35	5	0	156
	2	0	0	33	31	1	15	0	0	19	1	0	100
	3	2	0	2	44	0	82	0	0	78	0	0	208
	4	0	0	19	0	0	67	0	0	20	0	0	106
1960	1	0	0	33	13	0	6	0	0	207	0	0	259
	2	0	0	40	7	0	2	0	0	6	0	0	55
	3	0	0	13	0	0	228	81	0	121	2	0	445
	4	0	0	1	0	0	138	0	5	72	0	0	216
1961	1	0	0	0	29	0	1	0	0	54	0	0	84
	2	0	0	7	4	6	0	8	0	73	0	0	98
	3	0	0	14	2	0	90	0	0	17	0	0	123
	4	0	0	15	0	0	8	0	0	295	19	0	337

TABLE 10.—Continued.

Year	Quarter	Regions[1]											
		CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	SBS	Total
1962	1	0	0	10	0	0	1	0	0	204	0	0	215
	2	0	0	7	7	0	18	0	0	9	2	0	43
	3	0–	0–	26	1	0	240	0	0	56	23	0	346
	4	0	0	1	1	0	14	0	0	109	2	0	127
1963	1	0	0	50	0	0	62	0	0	3	0	0	115
	2	3	0	1	0	0	0	3	0	10	0	0	17
	3	0–	0–	1	0	3	54	0	0	49	0	0	107
	4	0–	0–	7	5	0	96	1	0	31	0	0	140
1964	1	0	0	1	0	0	0	0	0	229	0	0	230
	2	0	0	0	0	0	0	0	0	9	1	0	10
	3	0	0	4	0	0	22	0	0	159	0	0	185
	4	0–	0–	19	0	0	3	0	0	58	0	0	80
1965	1	0	0	2	0	0	5	0	0	7	0	0	14
	2	1	15	0	0	0	3	0	0	0	0	0	19
	3	0	0	7	0	0	4	0	0	429	1	0	441
	4	0–	0–	1	0	0	406	0	0	216	1	0–	624
1966	1	3	0	1	0	0	19	0	0	49	0	0	72
	2	0	0	10	0	0	1	0	0	2	0	0	13
	3	0	0	1	0	0	50	4	0	262	1	0	318
	4	0	0	1	0	0	238	4	0	87	2	0	332
1967	1	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	2	0–	0–	5	0	0	105	0	0	1,111	0	0	1,221
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	11	0	0	59	0	0	70
1968	1	0	0	0	0	0	0	0	0	0–	0–	0–	0
	2	0	0	2	0	0	5	1	0	0	0	0	8
	3	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
	4	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–	0–
1969	1	1	0	1	1	0	5	1	0	0	0	0	9
	2	0	0	3	0	0	10	3	0	30	0	0	46
	3	0	0	1	0	0	48	0	0	25	3	0	77

[1] CCI = Central California inshore
CCO = Central California offshore
SCI = Southern California inshore
SCO = Southern California offshore
SCS = Southern California seaward
BCI = Baja California inshore
BCO = Baja California offshore
BCS = Baja California seaward
SBI = South Baja inshore
SBO = South Baja offshore
SBS = South Baja seaward

ment between these values lends support to the idea that the method of data assembly causes little bias relative to size of the major fluctuations in anchovy larva abundance. Both the Spearman rank difference and the product-moment correlation coefficients are 0.99.

MacGregor (1968) suggested that the problem of determining the number of batches of eggs spawned per year per female is the major source of imprecision and bias in the adult biomass estimates from egg census and fecundity data. He further suggested that the best strategy for egg census would be to conduct an intensive cruise over a brief period in which no female is likely to spawn more than once. For the purpose of this paper, a preliminary judgment as to the importance of multiple spawnings in the larva ratio estimate of anchovy biomass may be made by comparing three models of spawning behavior. The first model is that the adult biomass is proportional to the regional census estimate. This model assumes that the product of the number of eggs spawned per ton of female, the number of spawnings per year, and the mortality rate of the larvae is stable. The second model is that each anchovy spawns once in the winter quarter. The third model is that each anchovy spawns in the single maximum quarter. Restated, the adult biomass is proportional to the 1) annual average regional census estimate of larval abundance, 2) winter quarter regional census estimate, or 3) annual maximum quarterly regional census estimate. The 1951-66 data for the Ahlstrom standard haul summation, the

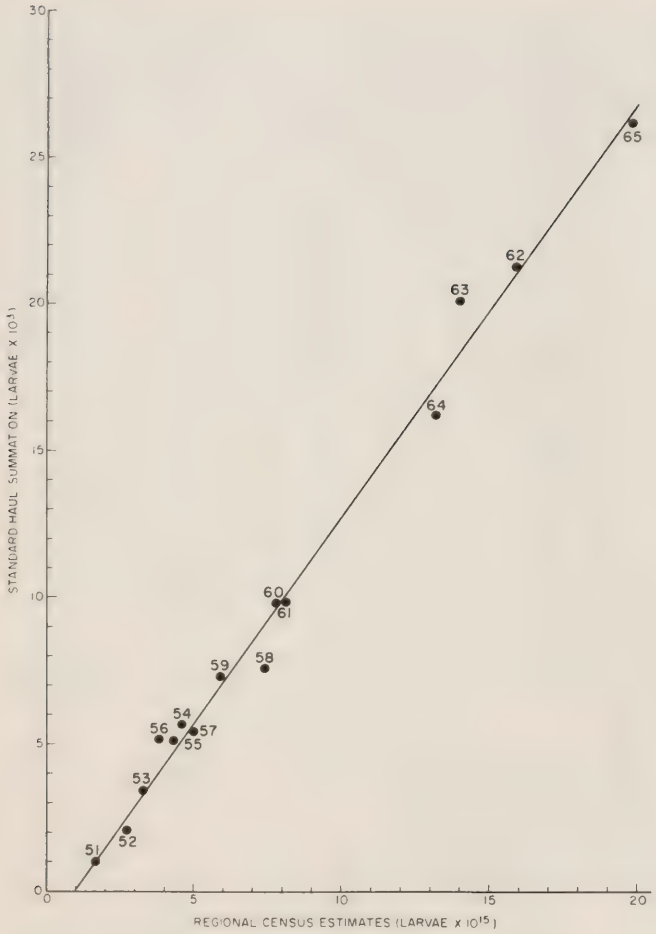

FIGURE 8.—A 16-year comparison of the regional census estimate derived for this paper and the standard haul summation quarterly average (Ahlstrom, 1968).

average regional census estimate, the winter spawning, and seasonal maximum are found in Figure 9. It is clear that the same trend and magnitude of increase are seen from each model. Since there is no obvious difference, the annual average regional census estimate of larva abundance will be used for the current biomass estimates.

It may be seen from Table 9 that the anchovy larvae have increased in number, particularly in the southern California section. Figure 10 illustrates the subdivision of the regional census estimate annual totals by section of the coast from 1951 to 1966. Within the southern California section, the inshore region was the dominant producer of anchovy larvae for the first 7 years. In the next 3 years, the southern California offshore became equally important in numbers of anchovy larvae. Between 1962 and 1965, the seaward region (160-280 miles off the coast) was a very important locality for anchovy larvae and this influence dropped radically to pre-1961 values in 1966 (Figure 11). This change and a smaller one inshore resulted in an appreciable lowering of the overall total in 1966 (Figure 10). The subpopulations of the northern anchovy have been assigned to coastal sections (Vrooman[5]; Vrooman and Smith, 1972),

[5] Vrooman, A. M. Anchovy subpopulations. Unpublished manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92037.

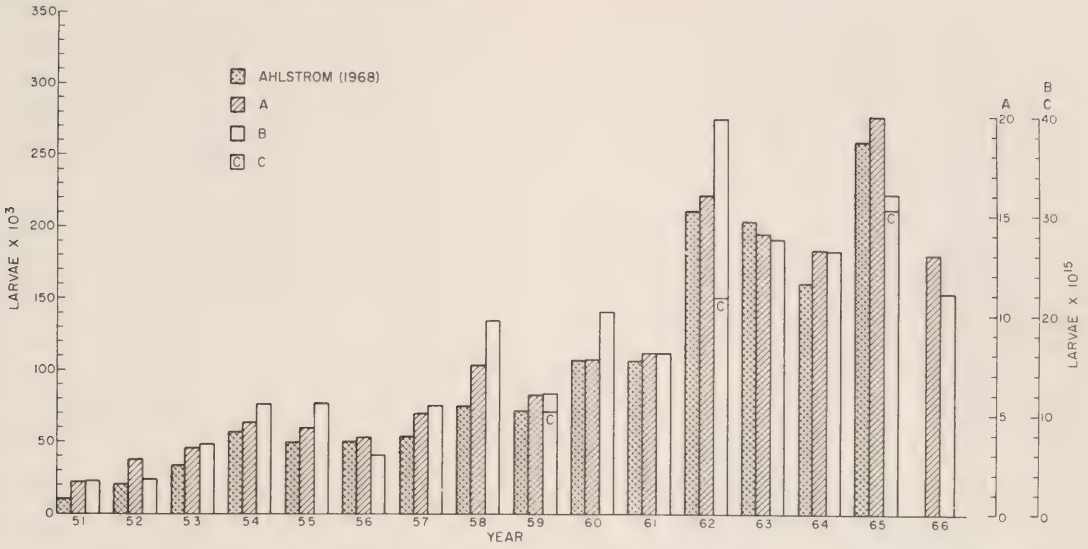

FIGURE 9.—A time-series comparison of the annual quarterly average standard haul summation (Ahlstrom, 1968, double cross-hatch) and the annual quarterly average regional census estimate ("C", clear bar including line C if any).

and the major portion of increase of northern anchovy is ascribed to the "central" subpopulation which spawns off southern California.

The seasonal contribution of anchovy larva abundance from 1951 to 1966 is illustrated in Figure 12. From 1951 through 1959, winter-caught larvae dominated the total. Beginning in 1960, spring larva abundance became increasingly important and, in 1962, substantially exceeded winter larva abundance. As mentioned above, the changing day-length in the spring quarter makes an appreciable difference for which the data have not yet been corrected. The spring-caught larvae are underestimated as a result. No correction has been applied for temperature- or food-specific growth rate changes, by season.

The increase of numbers of anchovy larvae shown in the foregoing regional census estimates could result from the traditional spawning areas being more completely covered with larvae, from new spawning areas being covered, or there being more larvae per unit area. There are instances of all three in the 1951-66 period. In particular, in the southern California section of the coast, where most of the increase took place, the primary effect has been the additional covering of traditional spawning areas. For example, in the southern California offshore region, April through June, 7 of 50 tows contained anchovy larvae in 1953, 25 of 48 tows contained larvae in 1955, and 51 of 53 tows had anchovy larvae in 1959 (14.0%, 52.1%, and 96.2% respectively). If one fits a regression line to the increasing proportions of positive stations with respect to anchovy larvae off southern California the slopes in percent per year from 1952 to 1966 follow:

	Winter	*Spring*	*Summer*	*Fall*
Inshore (0-80 miles)	1	2	1	1
Offshore (80-160 miles)	4	6	4	1
Seaward (160-280 miles)	2	7	2	1

Also, there are more anchovy larvae per positive station than before. In the years 1962-66 there are 5-8 times as many larvae per positive station as in 1951 (Table 11). The number of larvae per positive station is not independent of the proportion of positive stations. One interpretation of samples of larvae is that they are drawn from relatively small (100's of meters, Smith, in press) patches of larvae which are dispersing in such a way that they tend to overlap. For example, for randomly distributed

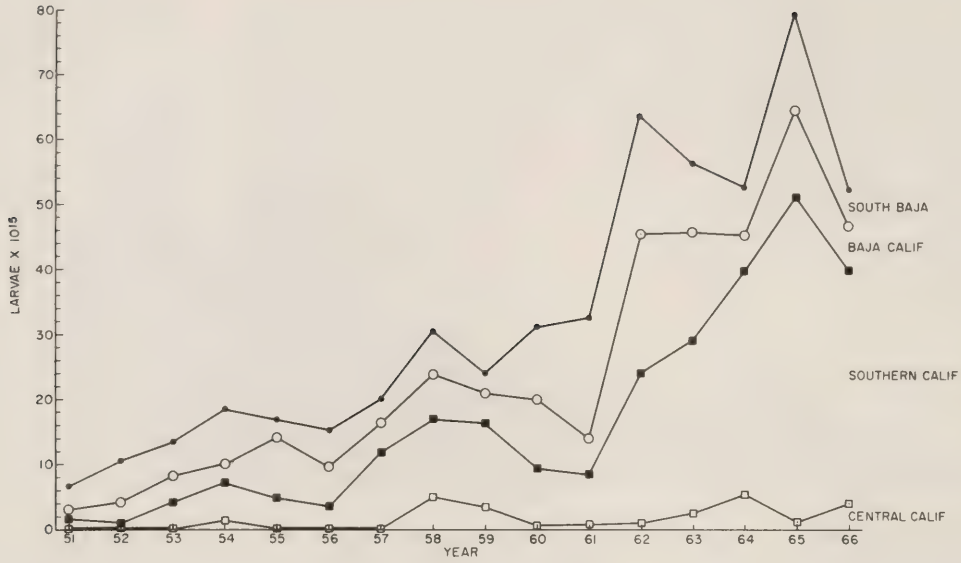

FIGURE 10.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by coastal section. The highest line (solid circle) is comparable to the quarterly average of "A" in Figure 9. The space between the top line and the line with open dots represents the contribution to the total by stations in the south Baja section. The space between the open dot line and the line connecting the solid squares represents the contribution of the Baja California section to the total. The space between the line connecting solid squares and the line connecting open squares represents the contribution of the southern California section. The space between the lines connecting open squares and the abscissa represents the contribution of the central California section to the total. For relative areas of the sections refer to Table 3 and Figure 2.

patches covering 0.1 of the area, the chance of encountering two patches is 0.01; with patches covering 0.9 of the area, the chance of encountering two patches simultaneously is roughly 0.8. In the southern California inshore and offshore regions, the proportion of positive stations is related to the number of larvae per positive station in the following way:

$$\log_{10} N_1 = 3.20\,P_1 - 0.218 \quad t = 11.17 \;\; 37\,\text{df}$$
$$\log_{10} N_2 = 2.13\,P_2 + 0.748 \quad t = \;\; 9.95 \;\; 37\,\text{df}$$
$$\log_{10} N_3 = 2.32\,P_3 + 0.573 \quad t = 14.40 \;\; 76\,\text{df}$$

where N_i = number of larvae per 10 m² per positive station in the ith region, when $i = 1$ = southern California inshore region, when $i = 2$ = southern California offshore region, when $i = 3$ the inshore and offshore regions are combined;

P_i = proportion of positive stations in winter and spring in offshore ($i = 2$) or inshore areas ($i = 1$), or both ($i = 3$).

If the patchy model applies, this set of equations is good only for the CalCOFI standard tow, in these two regions. For example on theoretical grounds, if the standard tow were to sample under 20 m² rather than the average 3 m² as at present, one would expect the proportion of positive tows to rise and the number per positive tow to decrease for any given average of anchovy larvae per total unit area.

In addition to an increasing proportion of positive tows in traditional spawning areas and increasing numbers of larvae per positive tow, the southern California seaward region is an example of a new spawning area being invaded in

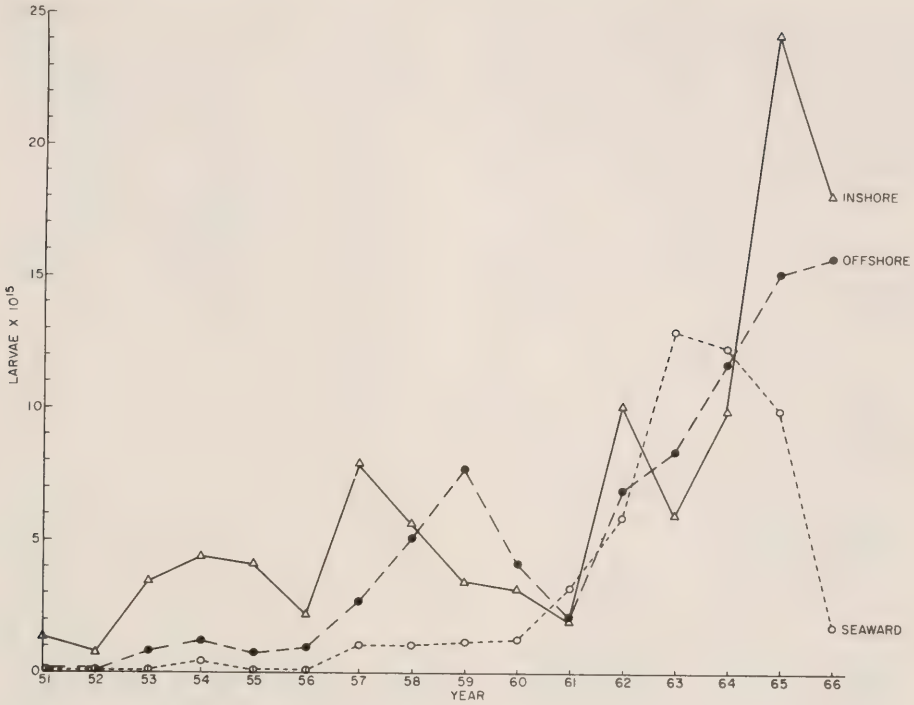

FIGURE 11.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by distance from shore within the southern California section. Lines connecting open triangles represent the southern California inshore, closed circles, the southern California offshore, and open circles, the southern California seaward. For relative areas of the regions refer to Table 3 and Figure 2.

the early sixties and becoming largely unused by the mid-1960's. The incidence of larvae has continued at less than 10% of the 1962 peak year in the southern California seaward region (Table 9).

THE CURRENT ESTIMATE OF ANCHOVY SPAWNING BIOMASS

The practice adopted in this paper for estimating anchovy spawning biomass consists of 1) regression estimates of the relationship between sardine larval abundance and Murphy's estimate (1966) of sardine biomass; 2) the ratio of anchovy:sardine larva abundance until 1958; 3) the regression estimate of the relationship between anchovy larva abundance between 1951 and 1958 and the sardine-derived anchovy biomass; and 4) the use of regression estimates to calculate anchovy and sardine biomass estimates outside the regression period. This differs from Murphy's (1966) method of using an anchovy:sardine ratio for each anchovy estimate. It also differs from Ahlstrom's (1968) method of tying each estimate to the biomass of sardine adults in 1958. Since regressions between two variables with time trends are influenced by the degree of temporal coherence of each variable, caution is warranted in their use. Confidence intervals may be calculated but their meaning is not clear due to the violation of the assumption of independence among the values used to calculate the regression. The regression estimates are used here as a simple shorthand method of reporting an apparent relationship.

The spawner biomass estimates of anchovy and sardine which result from this and previous

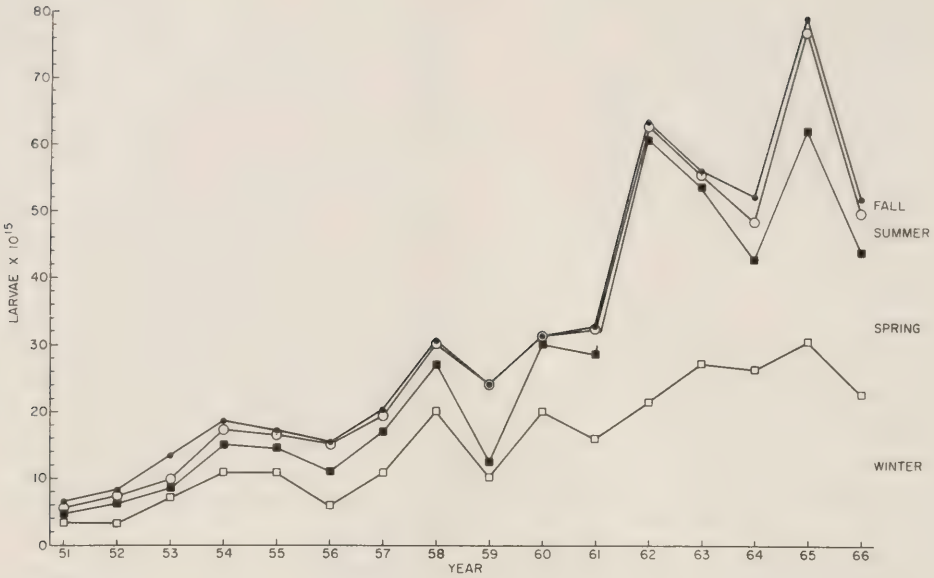

FIGURE 12.—A time-series comparison of the annual total regional census estimates of anchovy larvae as grouped by season of spawning. The highest line (solid circle) is comparable to that found in Figure 10 and to the height of "A" in Figure 9.

studies are found in Table 12. The primary objective of this study concerns the period of increase from 1951 to 1966. Despite various technical deficiencies in the basic data, the years 1940, 1941, 1950, and 1969 are also estimated in the section to follow.

The first column of Table 12, Murphy's (1966) sardine spawner biomass estimates, is reproduced without change. If those estimates are changed by later studies, all other values in the table must be adjusted. The important features of Table 12 are 1) a regression estimate to derive sardine spawner biomass estimates from the regional census estimates of total sardine larvae; 2) a ratio estimate of anchovy spawner biomass which is half the product of the anchovy:sardine ratio and the sardine biomass; and 3) a regression estimate of anchovy spawner biomass derived from the regional census estimate of total anchovy larvae.

The equation for a least squares estimate of sardine spawner biomass and sardine total larvae derived for this study is:

$$B_s = 0.230L_s - 0.057$$

where B_s is the annual estimate of sardine spawner biomass in thousands of short tons and L_s is the regional census estimate annual total of sardine larvae in numbers times 10^{12} in the years 1951-58, excluding 1953. The years 1953 and 1959 were eliminated as outlyers on a scatter diagram when it was found that the assumption of constant size distribution of larvae had been violated. The equation was later simplified by assuming a zero intercept to:

$$B_s = 0.206L_s$$

The anchovy spawner biomass estimates were derived from the ratio of anchovy:sardine larvae and the Murphy sardine biomass estimate in the following way:

$$B_a = c\left(\frac{L_a}{L_s} B_s\right)$$

where B_a is the ratio estimate of anchovy spawner biomass, L_a is the regional census estimate

TABLE 11.—Anchovy larvae per positive station.

Year	No. of positive stations	No. of anchovy larvae	No. of larvae per positive station
1951	344	26,951	78
1952	399	53,457	134
1953	539	85,178	158
1954	626	126,191	202
1955	558	134,017	240
1956	482	104,192	216
1957	518	135,966	262
1958	667	197,082	295
1959	729	182,176	250
1960	628	254,263	405
1961	420	88,925	258
1962	374	190,735	510
1963	370	172,611	466
1964	372	141,498	380
1965	392	234,850	599
1966	738	364,689	494

of anchovy total larvae, and c is a constant representing the relative fecundity of sardine relative to anchovy, here assumed to be approximately 0.5. Lenarz (1972) suggests a constant of escapement of 1.1 to counteract the tendency for anchovy larvae to pass through the mesh openings of the standard silk net to a greater extent than sardine larvae. This experimentally derived estimate from paired tows which captured both species in standard and fine mesh nets is considered too small to be appreciable on the scale of variability encountered in plankton tows. Murphy's (1966) estimate of the escapement factor, i.e., 2, is rejected.

The equation for a least squares estimate of the anchovy spawner biomass and anchovy total larvae is:

$$B_a = 0.094\, L_a + 0.072$$

defined in the same way as the sardine case above. Similarly, the zero intercept was forced, giving:

$$B_a = 0.098 L_a$$

which is the equation used for the regression estimate of anchovy spawner biomass.

The aberrant years 1953 and 1959 were recalculated assuming the slope and the Murphy sardine spawner biomass estimate are correct and that the sardine larva estimates are biased or imprecise. The recalculated estimates (parentheses, Table 12) appear to conform better to the trends of anchovy biomass and anchovy-sardine ratio.

The data from 1940, 1941, 1950, and 1969 have been manipulated to extend the biomass estimates. The 1940 and 1941 cruises were

TABLE 12.—Sardine and anchovy spawner biomass estimates by ratio and regression methods.

	Murphy sardine spawner biomass ($\times 10^3$T)	Regression sardine spawner biomass ($\times 10^3$T)	Sardine larval estimate ($\times 10^{12}$)	Anchovy larval estimate ($\times 10^{12}$)	Anchovy sardine ratio	Ratio anchovy spawner biomass ($\times 10^3$T)	Regression anchovy spawner biomass ($\times 10^3$T)
1940	1,296		1,634*	5,943*	3.64	2,359	
1941	2,001		2,476*	7,104*	2.87	2,871	
. . .							
1950	716		3,343	2,602	0.78	279	
1951	570	553	2,685	6,504	2.42	690	637
1952	554	542	2,633	8,132	3.09	856	797
1953	709	450	2,189 (3,442)**	13,632	6.23 (3.96)**	2,209 (1,404)**	1,335
1954	668	658	3,193	18,533	5.80	1,937	1,816
1955	425	404	1,959	17,100	8.73	1,855	1,676
1956	293	351	1,706	15,215	8.92	1,307	1,491
1957	212	234	1,137	20,040	17.63	1,869	1,964
1958	281	299	1,453	28,272	19.46	2,875	2,771
1959	190	117	570 (922)**	23,463	41.16 (25.45)**	3,910 (2,418)**	2,299
1960		201	975	31,414	32.22		3,079
1961		132	642	32,538	50.68		3,189
1962		151	731	63,758	87.22		6,248
1963		78	379	61,533	162.36		6,030
1964		104	505	52,253	103.47		5,121
1965		226	1,098	79,292	72.21		7,771
1966		151	735				
. . .				52,200	71.02		5,116
1969		27†	132†	33,623†	254.72†		3,293†

* 1940, 1941—larval estimates seasonally adjusted.
** Parenthetic numbers for 1953 and 1959 assume larval numbers biased.
† 1969—larval counts 75% complete; adjusted for extra retention of small larvae.

conducted during the sardine spawning season, but excluded an important portion of the anchovy spawning season. Similarly, the cruises only sampled 20% of the area we now consider routinely surveyed. The ratio of sardine and anchovy larvae was used for 1950 and will not be discussed further. The 1969 samples systematically violated the assumption of stable size composition of larvae.

The cruises of 1940 and 1941 were conducted over the southern California inshore and offshore regions in the spring and summer. The total for both species in both regions and in both years was derived by simulation of analogous cruises within the 1951-60 survey period and the product-moment correlation coefficient is listed for each species, for each region, and year.

Year	*Species*	*Region*	*Original*	*Seasonally adjusted*	*Correlation coefficient*
1940	Anchovy	SCI	1,545	3,229	0.794
		SCO	820	2,714	0.945
		Total	2,365	5,943	
1940	Sardine	SCI	502	726	0.794
		SCO	891	908	0.955
		Total	1,393	1,634	
1941	Anchovy	SCI	1,494	3,257	0.845
		SCO	2,104	3,847	0.962
		Total	3,598	7,104	
1941	Sardine	SCI	987	1,305	0.807
		SCO	1,161	1,171	0.981
		Total	2,148	2,476	

The ratio of this group of samples, within the same boundaries as the other regional census estimates used here, change from 1.70 to 3.64 in 1940 and change from 1.68 to 2.87 in 1941. Accordingly, these ratios are used in Table 12.

The 1969 data point for anchovy is modified in a crude attempt to adjust for the extra retention of anchovy larvae in a new sampling net (see Figure 4) which retains approximately 50% more larvae. The 1969 surveys were conducted with a 1-m net with 50% more open area, more regular mesh apertures, and an average mesh width of 0.505 mm rather than the 0.55 mm aperture silk net (used and wet). The effect of additional mesh on reducing the extrusion effect of filtration pressure is discussed in Tranter and Smith (1968).

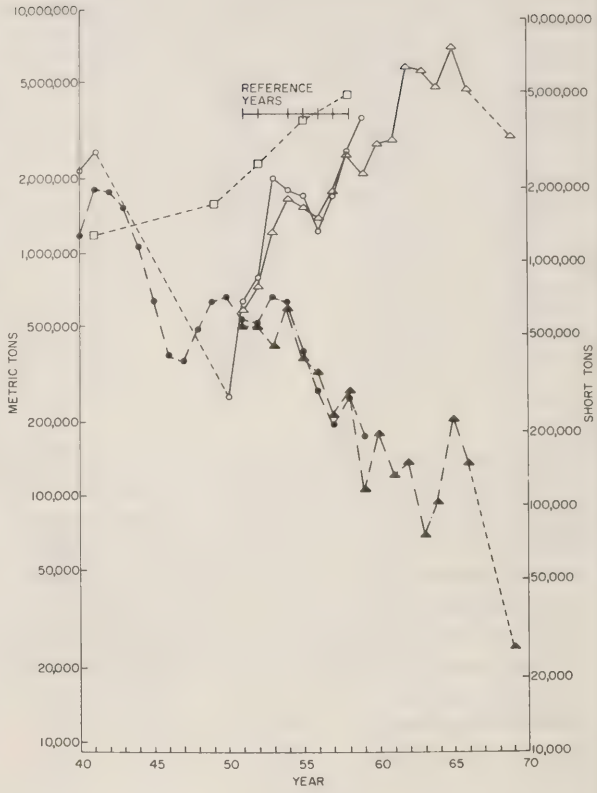

FIGURE 13.—A time-series comparison of sardine and anchovy biomass estimates from 1940 through 1969. The solid circle represents sardine biomass as calculated from the fishery by Murphy (1966) and extends from 1940 to 1959. The solid triangle represents sardine biomass derived from a regression estimate of the relationship between the Murphy biomass estimate and the annual total regional census estimate of sardine larvae during the reference years and is extended from 1951 through 1969. The open circle represents the estimates of biomass derived from the ratio of anchovy larvae to sardine larvae and the Murphy sardine biomass estimate from 1940 to 1959. The open triangle represents anchovy biomass derived from a regression estimate of the relationship between the anchovy tonnage calculated from the anchovy:sardine larvae ratio, and the annual total regional census estimate of anchovy larvae and extends from 1951 through 1969. The open squares represent the Murphy estimate of anchovy spawning biomass by 3-year averages (Murphy, 1966, Figure 17, p. 65). Dashed lines represent interpolations between nonadjacent years.

Figure 13 contains all the estimates resulting from this study. Murphy's sardine biomass estimates are plotted from 1940 to 1959. The anchovy biomass estimates derived from the anchovy sardine ratio and the anchovy larva regional census in 1940, 1941, and 1950 through 1959. The regression estimates are reproduced from 1951 to 1959 for comparison with the Murphy sardine biomass and ratio-derived anchovy biomass. The regression estimates of both sardine and anchovy spawner biomass are extended through 1966 and a tentative estimate for 1969 is placed for comparison.

DISCUSSION

Important changes in the size of the anchovy population have occurred in the California Current area over the past two decades. The increase of anchovy has coincided with the continuing decrease of sardine in the same area. All available evidence indicates that the anchovy and sardine populations declined between 1941 and 1951, and thereafter the anchovy underwent a sustained increase reaching a plateau of 5-8 million metric tons between 1962 and 1966. This population size may be between 2 and 3 times the anchovy spawning population of 1940-41 and between 5 and 10 times the anchovy population in 1950-51. Changes of this magnitude in the absence of a fishery underscore the importance of natural fluctuations in the population size of a fish species. Fishery management of such a species must be responsive to changes of this magnitude and rapidity.

Murphy (1966, 1967) speculated on the effect of the anchovy population on the recovery of the sardine population. Neither the feeding of anchovy and sardine nor the population dynamics of the food organisms is well enough understood in the California Current. Since the size frequency curves of larvae are relatively invariable (Ahlstrom, 1965; Lenarz, in press) one would expect competition, if any, to occur in the juveniles and pre-recruits of either species.

One interesting fact may be the decline of sardine spawning in the spring and summer has coincided with an increase of spawning in spring by the anchovy. In the estimates of spawner biomass of sardine and anchovy, no attention has been given the possibility that fecundity in numbers of eggs per batch and number of batches per unit time is plastic.

The numbers of anchovy and sardine larvae have been used here exclusively to describe changes in the adult biomass which spawned them. Since this process seems so effective, one might wonder what is required to refine techniques so that spawning, and larval and juvenile survival, may be used to predict the recruitment of year classes to the fishery. I believe the two major barriers are that 1) the size composition of the larvae of both species is so dependent on the sampling gear that mortality rates will remain too crude to project survival and 2) the effect of transport of larvae, particularly offshore to "unfavorable" areas, is neither well enough measured nor understood to effect predictive sampling systems.

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I would like to acknowledge the impact on my personal research and the effect on the overall study of environmentally induced natural variability that Dr. O. Elton Sette has had. The preparation of this paper would not have been possible without the aid and discussions of Dr. E. H. Ahlstrom. I would like also to acknowledge the assistance of my colleagues Dr. William Lenarz, David Kramer, and James Zweifel in compiling and editing this paper. Drawings and mathematical tables were prepared by James Thrailkill, Esther Barker, and Nancy Wiley. All biological specimens used were sorted and identified since 1940 by Dr. E. H. Ahlstrom and his staff.

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PRE-EXPLOITATION ABUNDANCE OF TUNAS IN THE EQUATORIAL CENTRAL PACIFIC

GARTH I. MURPHY[1] AND RICHARD S. SHOMURA[2]

ABSTRACT

The tuna resources and the environment in the equatorial central Pacific were investigated from 1950 to 1954. This report summarizes the data from these investigations and examines the distribution and relative abundance of tunas in relation to the environment.

The circulation of the waters of the equatorial region is described. The generally accepted view of a zonally oriented flow pattern of the South Equatorial Current between the equator and the Countercurrent is modified, and a model is proposed which regards the circulation as a series of homologous northwestward flowing cells. The evidence supporting this type of flow pattern is presented and discussed.

The variation in abundance of deep-swimming yellowfin tuna in space and in time is analyzed in relation to various environmental features. The hypothesis developed is that the change in abundance of yellowfin tuna is a function of the variation in the wind-driven ocean circulation and the attendant changes in the development of forage organisms.

A study of the distribution and abundance of surface tunas (skipjack tuna and small yellowfin tuna) revealed that more schools are sighted near land than in the open ocean. In the open ocean more tuna schools were observed in the countercurrent than in the zone from the equator to lat 5°N, where deep-swimming yellowfin tuna are most abundant. Rather than respond to the general level of standing crop of forage, the surface tunas appear to respond to secondary factors that make it possible to forage more effectively. The distribution of "fronts" is such a secondary factor influencing the distribution of surface schools.

In 1949, before the establishment of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu,[3] the tuna resources of the equatorial central Pacific were little known and even less well understood. In the eastern tropical Pacific the Americans had a highly developed fishery for surface schools of yellowfin and skipjack tunas, and in the western Pacific the Japanese had an active longline fishery for the larger subsurface tunas. In the central Pacific, however, information on the tuna resources was limited to the experiences of a few commercial operators who had prospected in the area.[4]

From 1950 to 1953 the Bureau of Commercial Fisheries surveyed this unknown area, roughly the region between long 120°W and 180°, and between lat 15°N and 10°S. Studies undertaken during this period involved the distribution of tunas, the productivity of the waters, and the circulation of the ocean. The results of the surveys of the tunas form the substance of this report. Although the other investigations are detailed elsewhere, they are brought to bear wherever they help to explain the distribution of the tunas. Studies in the equatorial central Pacific

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[2] National Marine Fisheries Service, Tiburon Fisheries Laboratory, Tiburon, CA 94920.

[3] Then called the Pacific Oceanic Fishery Investigations. The facility is presently known as the National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory.

[4] It should be noted that today (1972) the oceanwide longline fishery is fully developed (see, for example, Suda and Schaefer, 1965). The results reported herein are representative of "virgin stock" conditions, and it is highly unlikely that a similar assessment can ever be repeated.

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after 1953 focused on special problems (Iversen and Yoshida, 1956) and are not considered in this report.

This paper on the equatorial tuna is in part documentary and summarizes the results of the Laboratory's experimental fishing and scouting; however, the major effort is a review of the distribution of yellowfin and skipjack tunas as it relates to the distribution of properties in the environment. To a lesser extent, we discuss two other tuna species, the albacore and the bigeye tuna. The results suggest that the abundance of yellowfin and skipjack tunas in the region varies according to the properties in the environment. The variation in abundance of deep-swimming yellowfin tuna in space and time is relatable to variations in the wind-driven ocean circulation that alter the rate of enrichment of the euphotic zone. How albacore and bigeye tuna are related to the environment is less clear. The occurrence of these species in deeper water than yellowfin tuna suggests that other factors may be of greater importance. The apparent abundance of surface tunas is not believed to be closely related to basic enrichment; rather, it appears that secondary factors, such as food-concentrating mechanisms, are more important.

Most of the data in this report have been published. The fish distributions have been described by Ikehara (1953), Murphy and Shomura (1953a, 1953b, 1955), Murphy and Ikehara (1955), and Shomura and Murphy (1955). The oceanographic data were published by Cromwell (1951, 1953), Austin (1954), Cromwell and Austin (1954), Cromwell, Montgomery, and Stroup (1954), Stroup (1954), and Stroup and Austin (1955). The plankton catches were reported by King and Demond (1953), Hida and King (1955), and King and Hida (1957).

SAMPLING METHODS AND MATERIAL

Longlining, trolling, and surface sighting, the latter supplemented by occasional live-bait fishing, were used to assess the abundance of tunas. None of these was completely satisfactory, chiefly because no single type of gear sampled all species and sizes of fish within each species with equal effectiveness. Further studies will undoubtedly reveal additional weaknesses in our general assumption that catches represent relative density of tunas.

Longlining

More effort was devoted to longlining (Figure 1) than to the other sampling methods, mainly because it proved to be the best way to capture significant numbers of tuna systematically.

Figure 2 shows the type of longline gear used during the survey. Niska (1953) gave details of its construction and operation. Basically the gear consists of (1) a mainline suspended at intervals from buoys and (2) branch lines that hang from the mainline, each with a baited hook. The amount of tackle between two buoys is called a "basket."

The mainline hangs slack in the water, presumably in the shape of a catenary (Figure 2). Since the mainline was 384 m long and the buoys were generally spaced about 274 m apart, the deepest hooks should have fished at about 152 m and the shallowest at about 76 m. The gear, however, fished at shallower depths than the expected depth because of differences in the forces exerted on the buoys by wind and surface currents and on the mainline by the deeper, sometimes opposing currents. Consequently the deep hooks may frequently have fished as shallow as 76 m (Murphy and Shomura, 1955).

At a typical longline station, 40 to 60 baskets of gear were set in the early morning and retrieved in the afternoon.

The longline catches are presented as numbers of fish per 100 hooks. Valid comparisons of availability can be based on this statistic, provided the construction of the gear and the operational details remain constant. Fortunately all of the catches were obtained in a nearly standardized manner that satisfied most of the assumptions, e.g., construction did not vary, roughly the same amount of gear was fished each day, and the fishing schedule was the same each day.

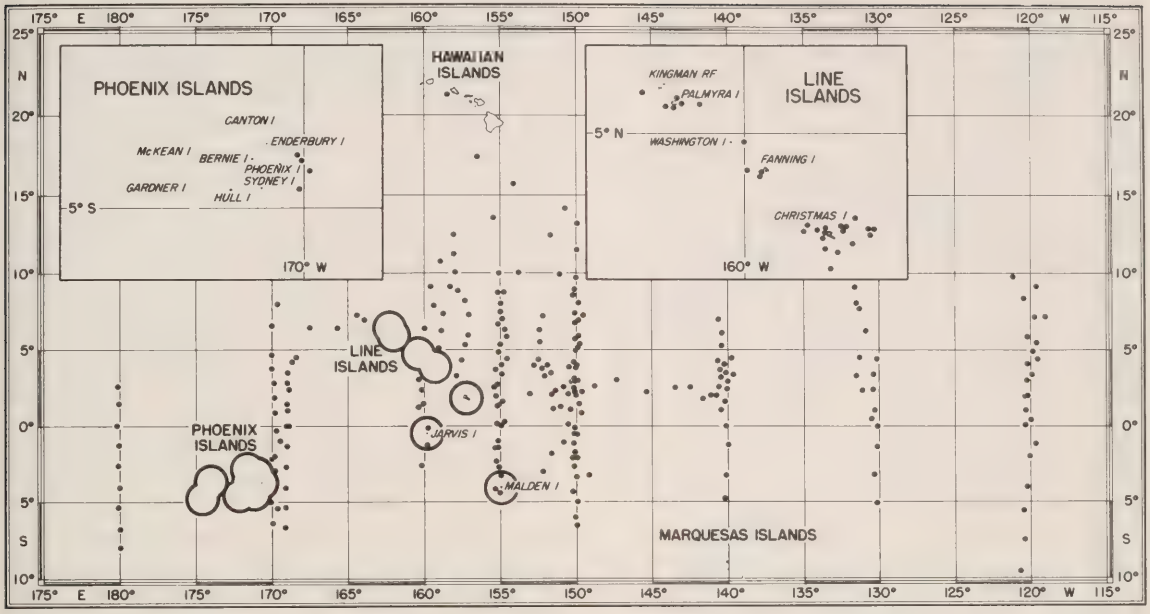

FIGURE 1.—Locations of longline stations. The circles show the location of an island or group of islands.

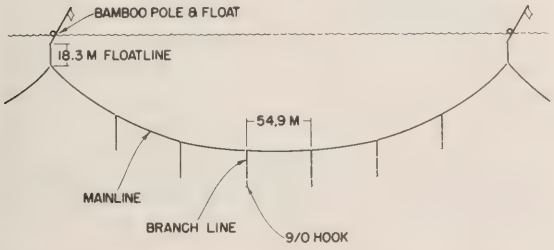

FIGURE 2.—Schematic diagram of tuna longline gear.

Trolling

Systematic trolling (Figure 3) provided another useful measure of tuna abundance. Generally when the vessels were underway (7-9 knots) two 45.7-m lines were trolled astern. A variety of tuna lures was used (Murphy and Ikehara, 1955). Occasionally near the islands, the "standard trolling" was modified by reducing vessel speed and trailing more than two lures. The catches from this type of fishing are considered separately from those of standard trolling.

Surface Sighting

As a further measure of tuna abundances, the abundance of surface schools of fish, bird flocks, and other signs of life was estimated by consistently maintaining a bridge log of sightings (Figure 3). A log of these observations was kept by the wheel watch under the supervision of the scientists on board (Murphy and Ikehara, 1955). These records provided a unique body of quantitative information on the bird and fish life in the central Pacific.

SPECIES OF FISH

Though the tunas are the most abundant and commercially most valuable of the large pelagic fishes in the central Pacific, a number of other species occupy prominent positions in the biota. The following list of species is largely based on longline catches, but it includes those likely to be captured by trolling or to be seen at the surface. The vernacular names listed below are used throughout the rest of this report.

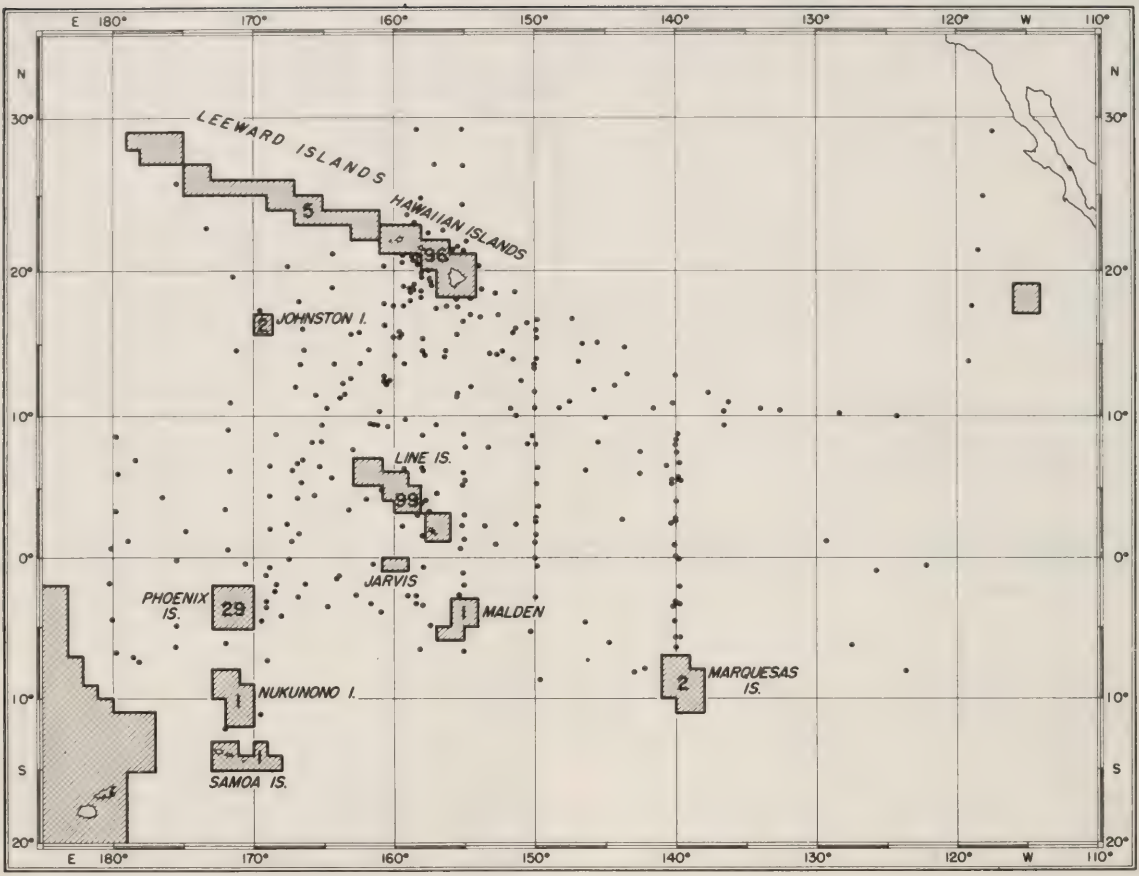

FIGURE 3.—Noon positions of vessels while trolling and surface sighting. Each dot represents the noon position for a day's observation. The number of days' observation in each of the shaded island areas (within 96.5 km of land) is shown by the figures. (Adapted from Murphy and Ikehara, 1955.)

Albacore, *Thunnus alalunga* (Bonnaterre)
Barracuda, *Sphyraena* sp.
Bigeye tuna, *Thunnus obesus* Lowe
Black marlin, *Makaira indica* (Cuvier)
Blue marlin, *Makaira nigricans* Lacépède
Blue shark, *Prionace glauca* (Linnaeus)
Dolphin, *Coryphaena hippurus* Linnaeus
Longnose lancetfish, *Alepisaurus ferox* Lowe
Mako shark, *Isurus* sp.
Oceanic whitetip shark, *Carcharhinus longimanus* (Poey)
Sailfish, *Istiophorus platypterus* (Shaw and Nodder)
Shortbill spearfish, *Tetrapturus angustirostris* Tanaka
Silky shark, *Carcharhinus falciformis* (Bibron)
Skipjack tuna, *Katsuwonus pelamis* (Linnaeus)
Striped marlin, *Tetrapturus audax* (Philippi)
Swordfish, *Xiphias gladius* Linnaeus
Wahoo, *Acanthocybium solanderi* (Cuvier)
Yellowfin tuna, *Thunnus albacares* (Bonnaterre)

ECOLOGICAL SUBDIVISION OF TUNAS

On the basis of size and behavior, populations of yellowfin tuna, bigeye tuna, and albacore can be conveniently separated into two groups: (1) the smaller surface fish and (2) the larger deep-swimmers. The two groups (Figure 4) cannot be readily sampled by any one fishing method; most surface fish are caught by trolling and live-bait fishing and most deep-swimmers by long-line. This situation evokes a query as to whether the separation represents a real difference in vertical distribution or whether the two apparent groups result simply because one type of fishing is more effective for small fish and one for large. The differences in catch rates on longline hooks fished at different relative depths (Table 1) strongly suggests that large tunas do, in fact, tend to spend their lives well below the surface. For instance, the catches of large yellowfin tuna on the deep and intermediate hooks were half again as numerous as on the shallow hooks. The differences were even more striking for bigeye tuna and albacore.

The separation of the population into two components, surface and deep-swimming, is accompanied by a horizontal dichotomy, at least in the instance of yellowfin tuna. Sightings and troll catches of small yellowfin tunas (<36.3 kg) were usually associated with emergent land or shoals (Murphy and Ikehara, 1955). As will be discussed later in the section on surface tunas, the longline when fished in such insular areas captures significantly more small fish (as small as 2.3 kg) than when fished in the open sea (>96.5 km from land). When moving away from land, the reduction in numbers of small fish in the longline catch is proportional to the reduction in school sightings which suggests that small yellowfin tuna are associated with land.

There is another difference between deep-swimming and surface tuna. Generally, surface tuna gather in compact schools, which occasionally contain thousands of individuals, whereas Murphy and Elliott (1954) provided evidence from the serial distribution of yellowfin tuna catches along the longline that deep-swimming yellowfin tuna gather in small schools. Little in their data, however, suggests that these groups

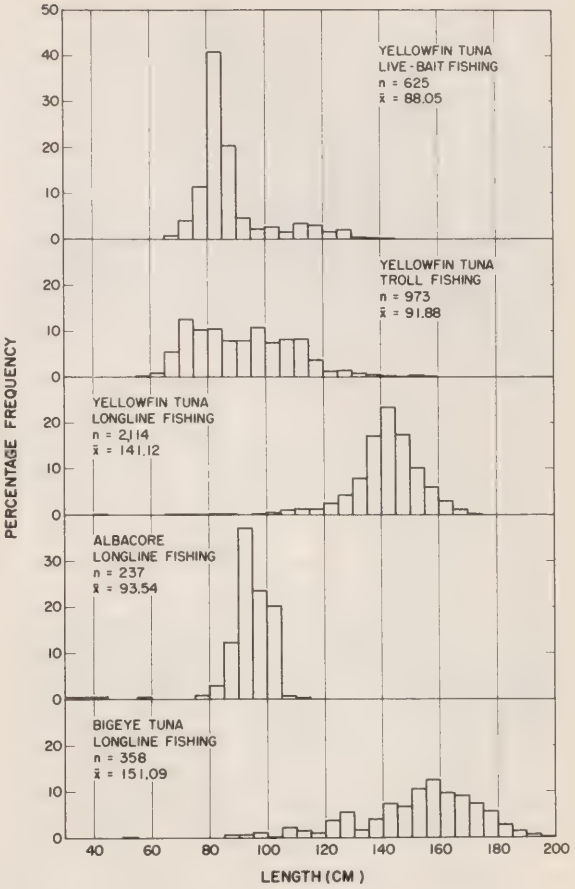

FIGURE 4.—Length frequencies (fork lengths) of the principal tuna species taken, by type of gear.

TABLE 1.—Yellowfin tuna, bigeye tuna, and albacore catches by relative hook depth (longline gear), 1950-53.

Tuna	Shallow	Intermediate	Deep	Total
Yellowfin	673	921	981	2,575
Bigeye	76	137	211	424
Albacore	10	68	122	200

are anything more than loose aggregations of a few large individuals. Thus both the degree of aggregation and the principal depth range differ with size of fish, at least insofar as yellowfin tuna are concerned. For these reasons it is convenient, and probably realistic, to treat the two categories separately.

DEEP-SWIMMING TUNAS

This section presents all the data on the distribution of deep-swimming tunas but emphasizes the yellowfin tuna and how the environment influences their distribution. Scientists have advanced certain hypotheses to explain the variations in the abundance of yellowfin tuna in the central Pacific (see, for example, Cromwell, 1953). These hypotheses, however, involve only portions of the total mass of data, and usually only a limited aspect of the variations in abundance, e.g., longitudinal variation.

The most elegant way to examine hypotheses about fish and the environment is to show step by step how precise interactions of energy flow and behavior (in a broad sense) result in a particular distribution of fish. This approach is not possible with the present data. Instead we have adopted the more generalized approach of advancing a hypothesis about one aspect of the data, i.e., the average distribution of yellowfin tuna with respect to the average distribution of environmental properties. Then we examine this hypothesis with respect to details of variation in abundance such as the north-south distribution and east-west distribution at particular times and places, and time variation at particular places. Our assumption is that if the same basic hypothesis stands up under this kind of cross-examination, its merit is essentially proved, even though a great deal remains to be learned about the exact way the ecosystem functions. This approach results in some repetition of arguments, especially as it has been possible to explain nearly all aspects of variation in abundance with the same hypothesis—namely, that variations in the dominant species, the yellowfin tuna, are influenced by variations in the wind-driven ocean circulation that affect the food supply of that species.

AVERAGE AREAL DISTRIBUTION

In this section we provide a brief description of the circulation of the major surface currents and the general distribution and relative abundance of the deep-swimming tunas and skipjack tuna in the central equatorial Pacific Ocean.

Oceanography

The dominant features of the eastern tropical Pacific are the three great currents (Figure 5): the westerly flowing North Equatorial Current

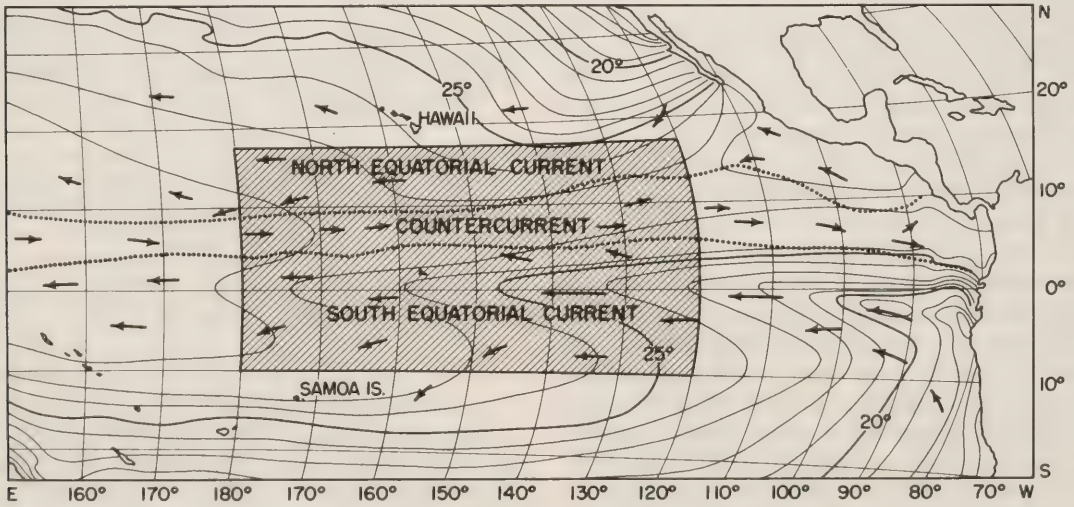

FIGURE 5.—Schematic representation of the major surface currents and surface isotherms in the central and eastern tropical Pacific. The area most intensively surveyed is shaded. Arrows denote approximate current direction. (Adapted from Schott, 1935.)

north of lat 10°N, the westerly flowing South Equatorial Current south of lat 5°N, and the easterly flowing equatorial Countercurrent lying between the two. Surface temperatures are generally high, mostly above 25°C.

Overlying the area are two major wind systems. The northeast trades blow over the North Equatorial Current and the southeast trades over the South Equatorial Current. Between them is a doldrum belt generally coinciding in latitude with the Countercurrent. The two equatorial currents are largely wind-driven, whereas the Countercurrent is simply the return flow caused by the piling up of the wind-driven water in the western portion of the Pacific. The speed of these currents at the surface is usually 1.85 to 3.70 km/hr (1-2 knots).

The configuration of the isotherms in Figure 5 shows that along any meridian the surface waters are cooler at the equator than in the adjacent waters to the north and south. This equatorial cooling is a result of wind-induced upwelling (Cromwell, 1953) and the divergence of water at the surface through the effect of the Coriolis Force. The Coriolis Force deflects the westerly moving water poleward, and this water is replaced by water rising from below (upwelling).

The equatorial upwelling, which brings deeper and enriched water upward into the euphotic zone, and the displacement of this water from the equator to a convergence south of the Countercurrent are the most important factors affecting the distribution of organisms in this region.

Tunas

The areal distribution of the large deep-swimming tunas can best be visualized from contour maps (Figures 6, 7, and 8). This series of diagrams was prepared from the catches of the Laboratory's longline fishing cruises (Figure 1) and the catches of several Japanese vessels (Murphy and Shomura, 1955; Shomura and Murphy, 1955). The presentation suppresses the random and temporal variability, yet it does convey the major features of the tuna distributions. It should be noted that the units used in contouring were those suggested by the catches.

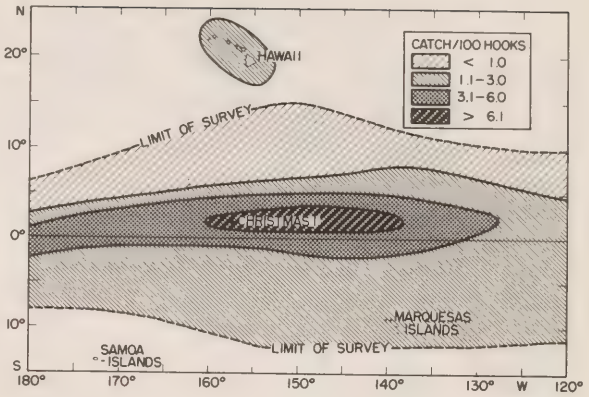

FIGURE 6.—The distribution of deep-swimming yellowfin tuna in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.

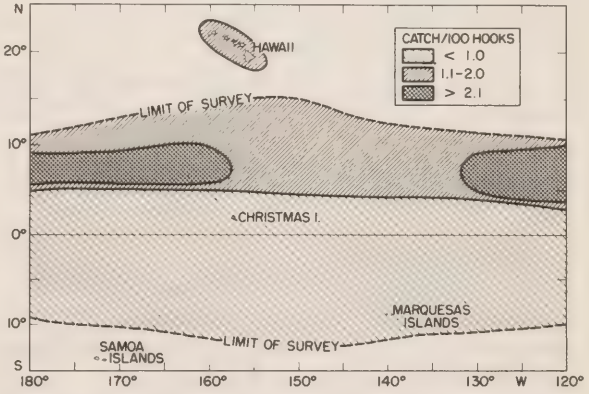

FIGURE 7.—The distribution of deep-swimming bigeye tuna in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.

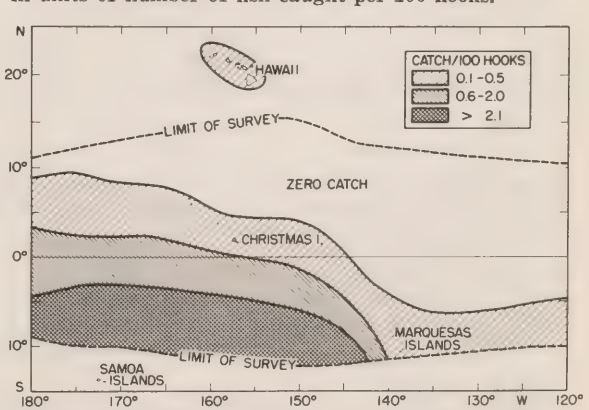

FIGURE 8.—The distribution of deep-swimming albacore in the equatorial central Pacific. The isograms are in units of number of fish caught per 100 hooks.

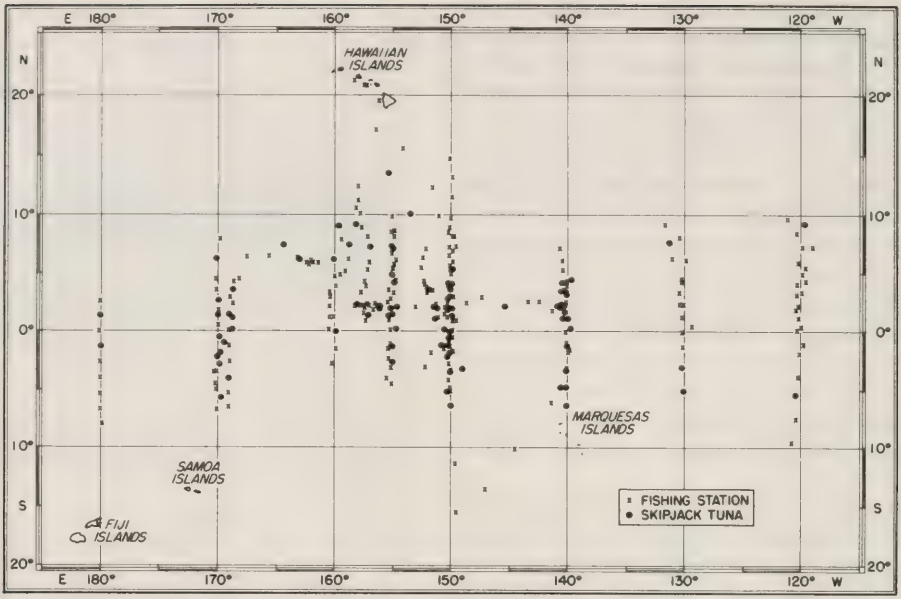

FIGURE 9.—The distribution of skipjack tuna in the equatorial central Pacific Ocean as shown by longline catches. A dot represents capture of one or more skipjack tuna.

Yellowfin tuna were found over the entire survey area (Figure 6), but the peak abundance occurred near the equator in the zone enriched by the equatorial upwelling. Between this zone and lat 10°N, the numbers decreased rapidly. Abundance south of the equator also declined but not as precipitously as to the north. Even near the equator this species was scarce at the eastern end of the survey area; it was most abundant in the center (between long 140° and 160°W) and somewhat less abundant to the west of long 160°W.

Bigeye tuna were not as abundant as yellowfin tuna, but their distribution, like that of the yellowfin tuna, was far more uniform over the area covered (Figure 7). On the basis of the small catches, two tongues of relatively high abundance were at the two ends of the survey area (Figure 7). These tongues, lying between lat 5° and 10°N, roughly coincide with the zone of the Countercurrent.

The distribution of albacore resembled neither that of the yellowfin nor the bigeye tunas. They were most numerous in the southwestern portion of the survey area (Figure 8) and their abundance declined to the northeast. Additionally, a broad zone to the north appeared to be completely devoid of the species. The reasons for this distribution are not at all clear.

In addition to the yellowfin tuna, bigeye tuna, and albacore that fit our definition of deep-swimming tunas, the longline captured a few skipjack tuna (Figure 9). The skipjack tuna is a smaller species (rarely over 18 kg) than the longline is designed to capture. Nevertheless, the gear is not absolutely selective because it has taken skipjack tuna as small as 2 kg.

The sporadic catches of skipjack tuna by longline are too scanty to estimate relative abundance and are therefore indicated in Figure 9 only as locality records. The skipjack tuna were present over a vast area of the central Pacific. Studies of the distribution of tuna larvae (Matsumoto, 1958) suggest that skipjack tuna are more abundant than yellowfin tuna in the central Pacific, the implication being that the equatorial central Pacific has a large underutilized stock of skipjack tuna.

SIZE OF DEEP-SWIMMING YELLOWFIN AND BIGEYE TUNAS

Though several species of tuna were taken by longline in the central Pacific, only the samples of yellowfin and bigeye tuna were substantial enough to warrant analysis of length differences by area. Iversen (1955, 1956) indicated that there were no significant changes in the size of yellowfin and bigeye tunas that could be related to time. Because of the wide temporal and spatial gaps in sampling, we confine ourselves to a descriptive summary of size differences with area. Most of the samples were taken between lat 5°N and 5°S and, as might be expected, no pronounced size differences were associated with latitude (only stations 96.5 km or more from land were considered in this analysis); only size differences associated with longitude are left for consideration.

To describe length differences more fully, we include data from the western Pacific (Murphy and Otsu, 1954) as material from the primary study area. We pointed out in an earlier paper (Murphy and Shomura, 1955) that the lengths of deep-swimming yellowfin and bigeye tunas differ across the equatorial Pacific. Since essentially the same gear has been used to sample the tuna in all areas, these changes must reflect some biological attributes of the populations.

Length frequencies for several longitudes shown in Figure 10 suggest a trend to smaller yellowfin tuna in the western Pacific. The essentials of the material in Figure 10, more succinctly shown in Figure 11, suggest a rather regular cline along the equator with respect to

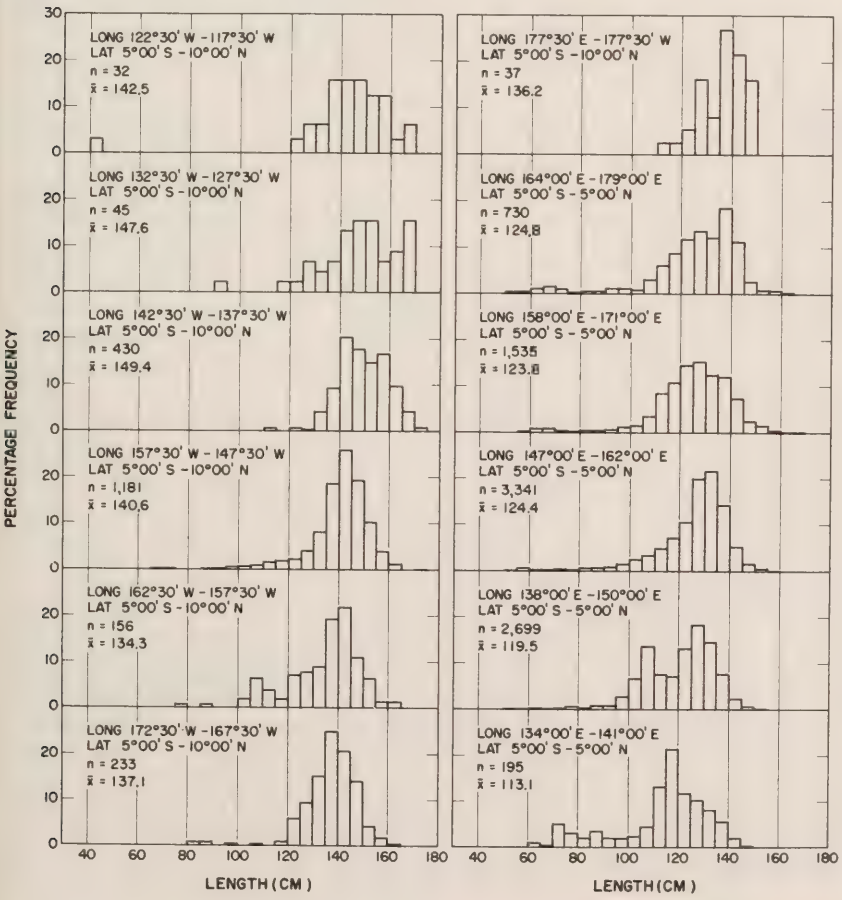

FIGURE 10.—Length frequencies of longline-caught yellowfin tuna by longitude of capture between lat 10°N and 5°S.

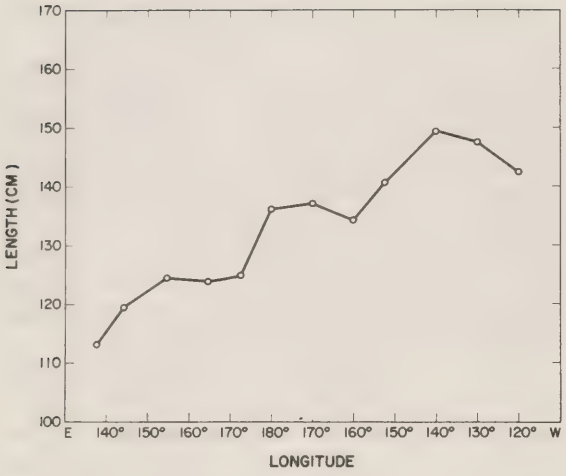

FIGURE 11.—Mean lengths of longline-caught yellowfin tuna.

average length. This same phenomenon is also evident for the bigeye tuna (Figures 12 and 13), which lends greater credibility to the view that the cline is not an artifact of the sampling system but due to a biological process.

This shift in length is reflected in other attributes of the populations. As indicated in Figure 14, males outnumbered females among the larger yellowfin tuna. Furthermore, the length at which males clearly dominate increases from west to east, as the average size of the fish sampled increases. Males also dominate the larger sizes of bigeye tuna (Otsu, 1954; Shomura and Murphy, 1955) but our data for this species are not adequate to examine the possibility that the length at which males dominate changes from west to east.

In addition to these clines, Royce (1953, 1964), in a study of yellowfin tuna morphometrics, dem-

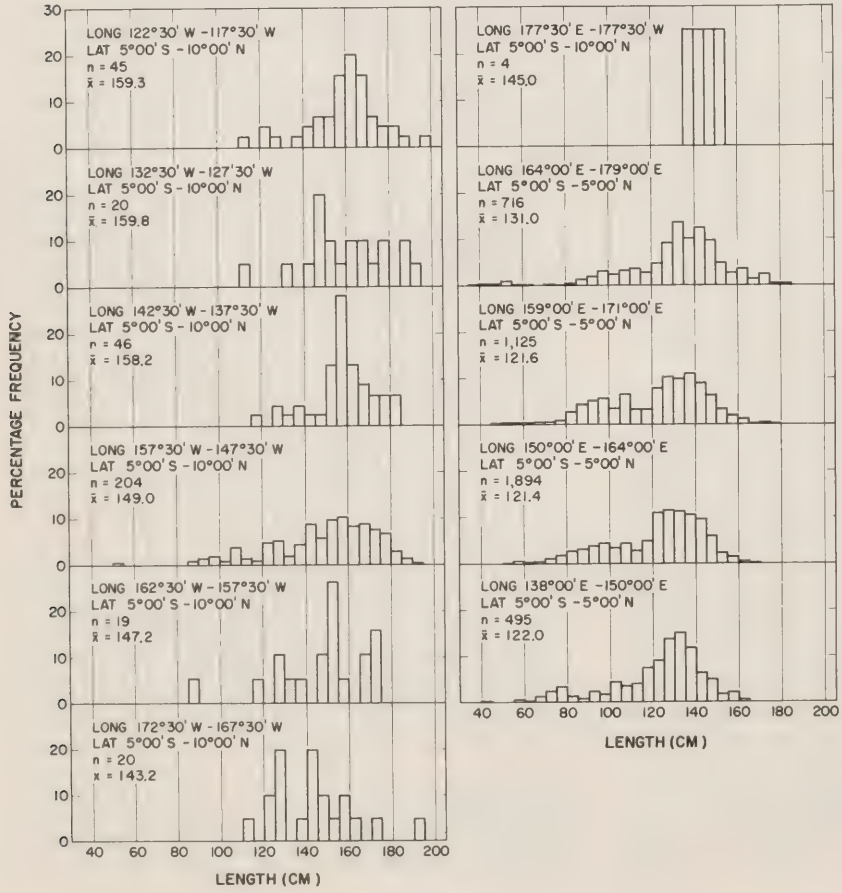

FIGURE 12.—Length frequencies of longline-caught bigeye tuna, by longitude of capture, between lat 10°N and 5°S.

onstrated east-west clines in the body proportions of yellowfin tuna taken in equatorial waters. For example, fin lengths decreased and head lengths increased to the east. Thus, along the equator we find more or less uniform clines in the yellowfin tuna of such biological characters as size, size at appearance of sex-ratio variations, and morphological characters. Limited evidence also suggests that the same phenomena are present in the bigeye tuna.

Inquiry into the basic causes for the east-west clines is somewhat speculative at the present time. Royce (1953, 1964) considered the morphometric evidence and concluded that the equatorial yellowfin tuna are made up of semi-independent stocks. Iversen (1956) focused his attention primarily on east-west size differences and suggested that the differences are maintained by easterly migration as the fish grow larger. An additional factor entering Iversen's hypothesis is that the number of small yellowfin tuna around the Line Islands, the only islands in the immediate vicinity of the equatorial central yellowfin tuna population, does not appear to be large enough to account for the sizable numbers of large deep-swimming yellowfin tuna in this general area, inferentially suggesting that recruitment must involve migration from somewhere else—the west, according to Iversen.

Conceivably recruitment could occur by movement of yellowfin tuna in a north-south direction, for there are large numbers of small islands in French Oceania, some 1,112 km (600 miles) to the south of the equatorial area. Small yellowfin tuna are known to occur near the surface around those islands (Royce, 1954), and the populations there, if extensive, could supply the necessary recruits to the large population of deep-swimming yellowfin tuna. This postulated movement, however, would be contrary to the conclusion reached by Royce (1964, p. 427) that "... most yellowfin tuna probably remain within a few hundred miles of where they occur as post larvae."

The length gradient of deep-swimming fish, with the attendant dearth of large fish in the west and small fish in the east, remains a strong argument favoring extensive west-east migration. If it is argued that there is no migration

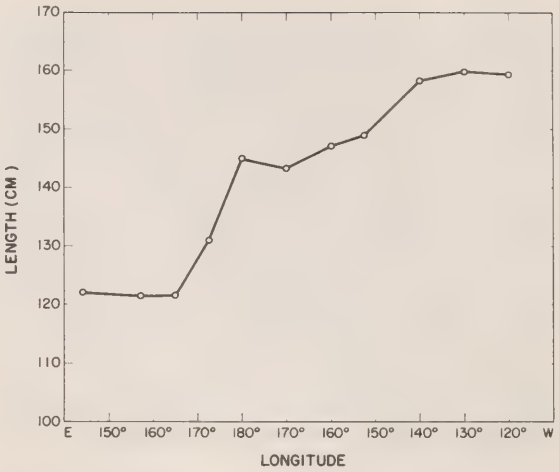

FIGURE 13.—Mean lengths of longline-caught bigeye tuna.

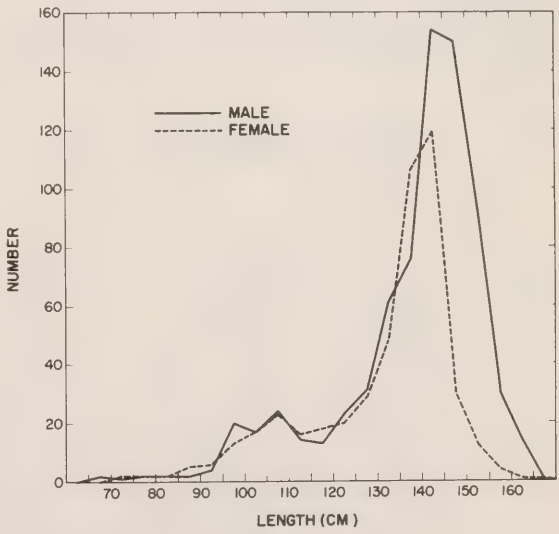

FIGURE 14.—Length distribution by sex of longline-caught yellowfin tuna (data from catches made in 1953).

and that the gradient exists simply because yellowfin tuna grow more slowly in the west, where the basic productivity is lower (Murphy and Otsu, 1954), there remains to be explained the relative scarcity of medium-sized fish in the eastern catches of deep-swimming tunas. This difficulty could be overcome by proposing that the

adoption of the deep-swimming habit is age-specific rather than size-specific and that the smaller fish are scarce in eastern longline catches because they are not old enough to adopt the deep-swimming habit. This proposal is not as farfetched as it might seem, for albacore appear to adopt the deep-swimming habit at a size (about 13.6 kg) at which yellowfin tuna still school at the surface. Furthermore, the fact that the size at which males dominate the catches increases, as the average size of the individuals in the deep-swimming population increases (Figure 14) argues against migration and suggests that at least some physiological changes are age-specific. Behavior changes might easily be among these age-specific attributes.

In summary, there are east-west clines in morphological and other biological characters of the catches. These clines can be explained by migration, if one chooses to ignore the evidence of morphometry and the changes of size at the onset of male dominance. If the clines are attributed to genotypic or phenotypic changes in relatively sedentary stocks, all available evidence can be accepted, but additional assumptions such as slower growth rate in the west and age-specific behavior changes must be introduced.

MERIDIONAL DISTRIBUTION

In a preceding section we examined the ocean and the fish populations in plane view and concentrated on the descriptive aspects. Most of the prominent features of the environment and the fish populations are zonally aligned, and the relations among the several fields can be most effectively visualized when their properties are examined in a meridional section. In presenting the details of the oceanography, the tuna distribution, and the tuna-oceanography interrelation-

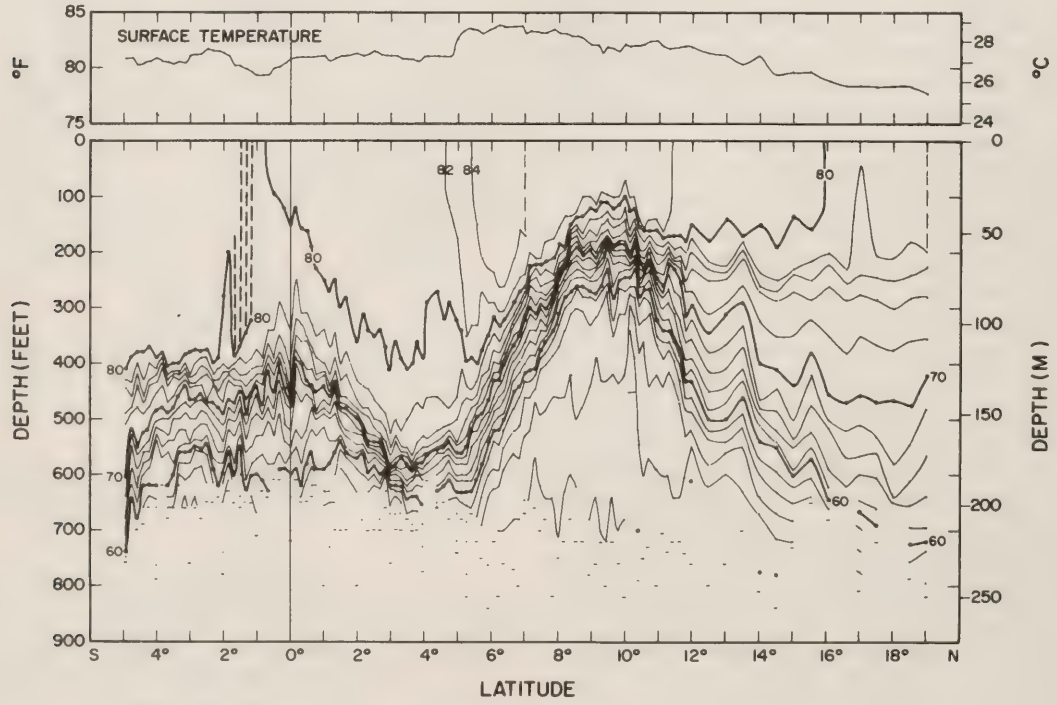

FIGURE 15.—Meridional temperature section based on bathythermograms, *Hugh M. Smith* cruise 11 along long 150°W (Austin, 1954b).

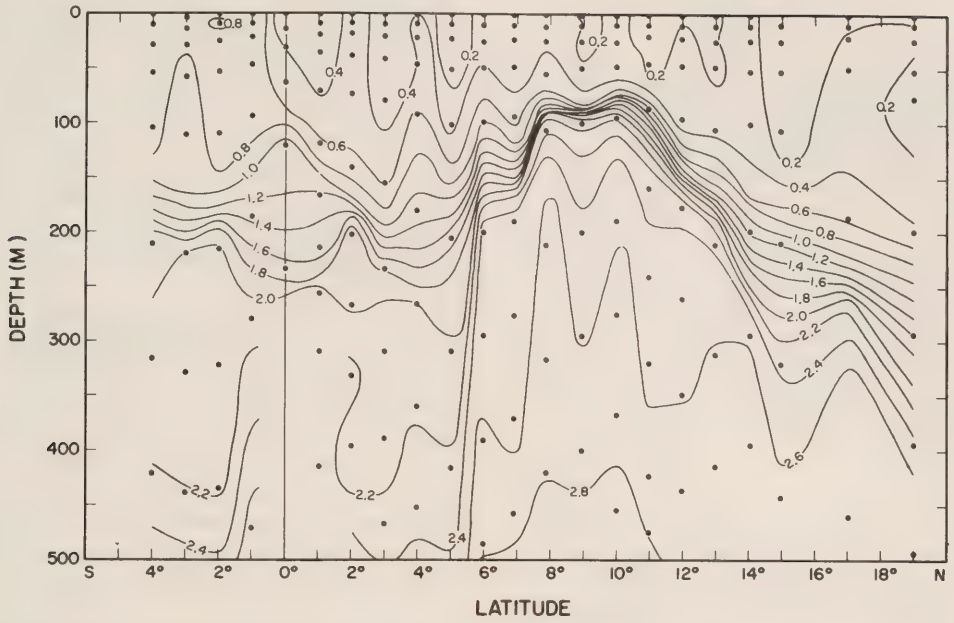

FIGURE 16.—Distribution of inorganic phosphate along long 150°W, September 26 through October 4, 1951, *Hugh M. Smith* cruise 11. PO_4 in micrograms per liter, isopleth intervals 0.2 μg atom per liter (Austin, 1954b).

ship, we have elected to use long 150°W, because more information is available from that meridian than from any other and it lies in the center of the region in which yellowfin tuna are most abundant (Figure 6).

Oceanography

A meridional temperature section along long 150°W (Figure 15) clearly shows the several features described in plane view (Figure 5). North of lat 10°N the isotherms sloping to the right indicate the westerly flowing North Equatorial Current. Between lat 10° and 5°N the isotherms slope to the left, indicating the easterly Countercurrent. South of the Countercurrent lies the westerly flowing South Equatorial Current.

The cool water at the equator is the result of divergence which disturbs the stability of the thermocline and thereby increases the rate of upward diffusion (upwelling). Under these conditions the surface waters are always cooler than adjacent waters. Nutrient salts, such as phosphate (Figure 16), are also affected, and their distribution suggests that nutrients are diffusing into the euphotic zone near the equator faster than they are being utilized. According to Cromwell (1953), these enriched waters moving northward and southward within the framework of the westerly flow are warmed and the nutrients are utilized by organisms.

Between the upwelling at and near the equator and the southern boundary of the Countercurrent at about lat 5°N (Figure 15), there is convergence and sinking of the northward flowing waters (Cromwell, 1953). The downward sloping arrows in Figure 17 show schematically the convergence with its attendant sinking. Among other features shown in the figure are the easterly flowing Countercurrent (flow is toward the observer), the westerly North Equatorial Current to the north, and the westerly South Equatorial Current to the south. The figure also

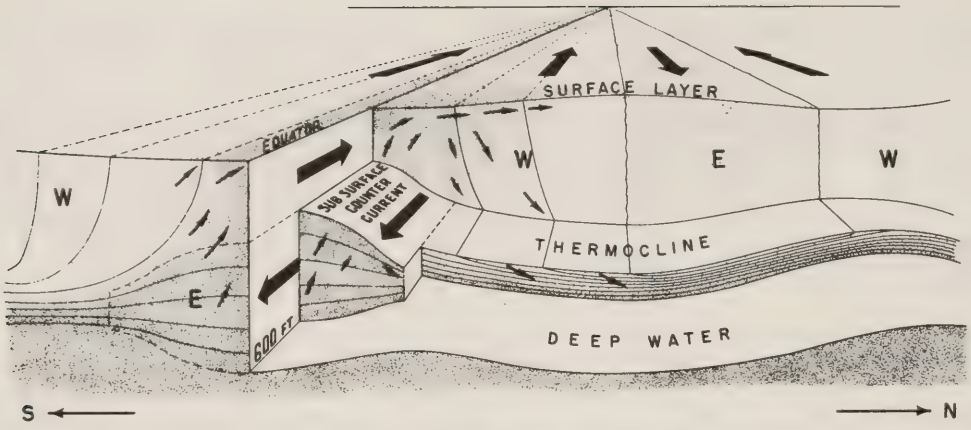

FIGURE 17.—Schematic representation of a meridional section of the equatorial central Pacific (Sette and staff of P.O.F.I., 1954, p. 3).

shows a feature new to this discussion, the Equatorial Undercurrent described by Cromwell, Montgomery, and Stroup (1954). This latter current is usually found in the upper portion of the thermocline and rarely flows as a surface current.

Tunas

Our aim is to compare the meridional distribution of fish with certain properties in the environment. Ideally, we should compare the weight of fish life at a given trophic level with such elements as plankton abundance and nutrient level. This comparison is difficult with the material at hand, but, as shown in Appendix A, the catches of yellowfin tuna, the dominant species, appear to reflect the abundance of the larger predators.

Tuna-Oceanography

In the discussion of the areal distribution of tunas we pointed out that the peak abundance of yellowfin tuna was near the equator. We now propose to examine the hypothesis that this striking concentration of yellowfin tuna is the result of the following sequence of events: (1) upwelling at the equator, (2) northward displacement of the water, (3) relatively rapid development of zooplankton, (4) a slower development of tuna forage, and (5) congregation of tuna in the region best supplied with forage.

It can be inferred from the distribution of yellowfin tuna and water temperature in Figures 6 and 15 that there is a general coincidence between the location of upwelling and the zone in which yellowfin tuna are most abundant. Figure 18 clearly shows this relation as well as the distribution of other variables such as plankton and current direction.

In the top panel (A), the temperature structure shows the cool surface waters at the equator that can be attributed to upwelling. That this is accompanied by enrichment was shown in Figure 16 in the distribution of inorganic phosphate. The sharp downward slope of the isotherms between lat 5° and 9°N is the region of the Countercurrent.

The second panel (B) shows the drift of the longline while in the water. This drift, which is essentially the movement of the gear between 0600 and 1600 hr, shows the direction of the several major water movements discussed earlier. North of lat 9°N, the drift is to the west, indicating the North Equatorial Current. Between lat 5° and 9°N, the drift is to the east, suggesting the Countercurrent. Except for the station nearest the equator, the drift is westerly south of lat 5°N, indicating the South Equatorial Current. The easterly drift at the equator is

probably caused by the easterly flowing Equatorial Undercurrent (Figure 17). It should also be noted that each side of the equator has a poleward component to the longline drift. These observations confirm empirically the conclusion by Cromwell (1953), based on theoretical considerations, that divergence at the equator leads to upwelling and that this enriched water moves poleward.

In the third panel (C), zooplankton is shown to be most abundant at the center of upwelling, falling off more precipitously to the north than to the south. The zooplankton reaches a maximum at or near the equator, where the upwelling is centered (panel A). The model proposed by Cromwell (1953) requires a net transport of water away from the equator, and because the zooplankton sampled is at least one trophic level removed from chemical nutrients, we might expect its peak abundance to be significantly displaced from the site of upwelling. The magnitude of the displacement would be a function of the rapidity with which the zooplankton reaches a peak, the speed of the north-south transport, and possibly the rate of grazing.

Since no displacement was observed in a series of stations spaced at 96.5-km intervals, the possible conditions include: (1) the zooplankton develops very rapidly, (2) the north-south transport is slow, (3) grazing is highest just north and south of the equator, or (4) a combination of the three factors. Nothing is known of the development rate of equatorial zooplankton (chiefly copepods), but some marine cladocerans have been reported (Wickstead, 1963) to reach a peak in 36 to 40 days at temperatures higher than 28°C. Assuming this rate of development for the equatorial zooplankton, a poleward displacement of water as rapid as 6.4 km a day would be readily detected in plankton hauls spaced 96.5 km apart. The lack of a displacement suggests that grazing may be an important factor controlling the spatial distribution of the standing stock of zooplankton in equatorial waters.

In addition to the lack of horizontal displacement of the peak of zooplankton from the equator (Figure 18), the plankton volumes south of the equator were slightly larger than those to the

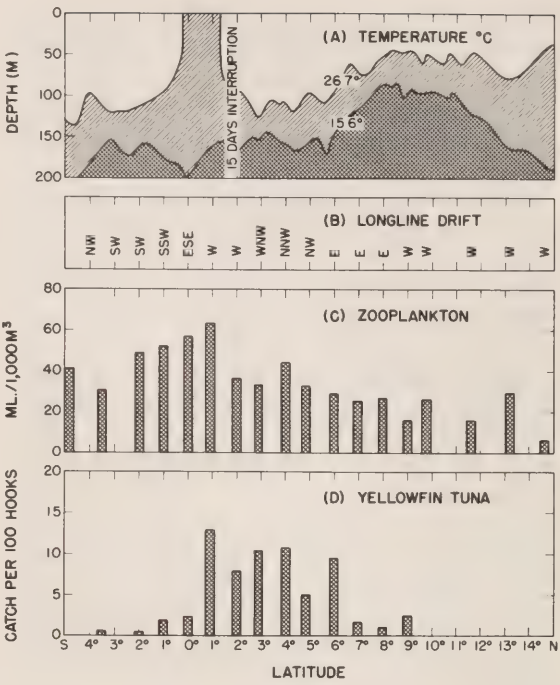

FIGURE 18.—Diagrams of several fields resulting from a section along long 150°W in September 1951. A. Temperature section from bathythermograms. B. Direction of longline drift at each fishing station. C. Volumes of zooplankton at each fishing station. D. Catch rate of yellowfin tuna at each fishing station. (Adapted from Sette, 1955.)

north. This situation, however, is not the usual one because King and Hida (1957) reported that the average standing crop of plankton is greater between lat 1.5°N and the southern boundary of the Countercurrent (about lat 5°N) than between lat 1.5° and 5°S. This general situation is thought to be the result of the dominance in this region of the central Pacific southeast trades which, according to Cromwell (1953), transport most of the enriched water northward. In the present instance, the longline drifts (Figure 18, panel B) give evidence that the momentary major transport was to the south of the equator. Thus, the observed asymmetry of the plankton is consistent with the momentary circulation.

The yellowfin tuna catches (Figure 18, panel D) show even less symmetry about the equator

than the plankton. This asymmetry seems anomalous until it is considered in the light of the general northward transport of the enriched water and the probable time required for tuna forage to appear after the enrichment at the equator.

Tunas do not consume the smaller zooplankters that make up the bulk of the catches of the 1-m nets of 30×××× gage mesh used to sample zooplankton. Rather, tunas forage on the higher trophic levels, from euphausiids to all but the largest nekton (Reintjes and King, 1953). If the food supply is the chief determinant of tuna abundance, the tunas, which are capable of rapid and extensive migration, will concentrate where they can most readily obtain food. In the absence of poleward motion we would presume that tuna forage as well as tunas would concentrate or develop at the equator, where the enrichment and the zooplankton are centered. There is poleward motion, however, and the successive trophic levels above the zooplankton would be expected to have their greatest population density at some distance from the equator.

SPACE AND TIME VARIATION

In this section we focus attention on the variation in the distribution of yellowfin tuna and the variation in distribution of properties in the environment and attempt to show their relation. The zone between the equator and the Countercurrent receives primary attention simply because more information is on hand from this area than from others.

Space and time variation in the tuna distribution have been discussed in earlier publications. Murphy and Shomura (1953b) pointed out that when and where southeast winds prevailed the yellowfin tuna seemed to be concentrated north of the equator; when northeast winds prevailed the yellowfin tuna were concentrated south of the equator; and during periods of variable winds they straddled the equator. These observations were amplified and further discussed by Sette (1955, 1958), who suggested that the average distribution of the catch rates might well be a function of geographical variation in the strength of the trades, if a suitable but unknown lag period is assumed between maxima of upwelling and the occurrence of tuna forage.

The waters of the equatorial current system are in a state of constant flux, with upwelling, poleward motion, sinking, and westerly motion integrated into a whole that represents a continuously changing environment. In this environment we have made "instantaneous" observations at selected points and times, and as expected the data obtained are dissimilar in respect to space and time. In theory, at least, a true concept of the relative magnitudes of the several components of the water motion should make it possible to unify these results into a coherent whole. It appears that vertical motions (upwelling) and sinking (convergence) are counterbalancing within the geographical limits (north-south) of the area under consideration, but the relative strengths of the westward and northward motions, which cannot be counterbalancing, have not been adequately defined.

Sette (1958), in interpreting the then available information, assumed that the western component of flow near the equator was of overriding importance in comparison with the poleward flow associated with divergence and upwelling. This assumption is consistent with the mean surface flows indicated in climatological-type summaries of ship's drift observations (e.g., Figure 5) but is not consistent with certain empirical determinations derived from the drifts of longlines and drogues. These determinations suggest that the average poleward component of motion to the north of the equator on long 120°W would bear little relation to events at lat 5°N on long 140°W and even less to events at lat 5°N on long 150°W. In other words, water parcels upwelled at the equator on long 120°W are probably lost from the system by the time they are transported westward to long 130°W, because their northward motion will have carried them to the Countercurrent (near lat 5°N). Here, they must sink because the Countercurrent is warmer and less saline than the waters to the south.

Most of the evidence for these arguments lies in measurements of the drifts of sets of longline

gear. The longline, which is suspended from the surface to the thermocline, gives a useful measure of the net movement of the mixed layer. Between the surface and the thermocline are about 512 linear meters of 0.635-cm diameter cotton line having about 10.2 sq m of surface for each basket of gear. The buoys that support the line are acted on by the wind, but they present only about 0.56 sq m of surface to each basket of gear. Typical sets consist of 40 to 60 such units, which are in the water about 10 hr. Since the gear is set at dawn, the morning fixes based on celestial navigation provide a good starting point. Because the last unit (first one set) is retrieved at about 1600 hr, it is necessary to rely on sun lines, dead reckoning, and the evening stars for the final position determination.

This procedure is routine during longline fishing surveys, but most determinations of drifts of the gear are somewhat unreliable for various reasons. There are, however, 14 measurements from the area between long 140° and 155°W and between the equator and lat 5°N that appear reliable within the limits of celestial navigation. These given a mean northward motion of 0.67 km/hr (0.36 knot) and a mean westward motion of 1.06 km/hr (0.57 knot), or a ratio of 1 to 1.6. Wind effect on the longline sets is unknown, but the relative amount of exposure to the two forces and the relative viscosities of the water and air suggest it is negligible. It can also be argued that the sample of 14 measurements is inadequate, and this cannot be denied. The 14 measurements were, however, well scattered in time and space and vary so markedly from pilot-chart summaries that we feel a revision of the existing concept is in order.

In addition to the longline drifts, special measurements of the motion of the surface water north of the equator were made in August 1952 by using drogues (Cromwell, Montgomery, and Stroup, 1954). A surface drogue placed in the water at lat 0°01'N, long 149°31.5'W, moved to lat 2°48.5'N, long 151°42'W in 10 days. The mean westward component was 0.85 km/hr (0.46 knot) and the northward component 1.18 km/hr (0.64 knot), values that are relatively consistent with the longline drifts.

Such high rates of northward flow seem to imply an exceedingly rapid rate of upwelling, which should possibly be characterized by an even more marked cooling at the equator than is indicated by the measurements at hand. In this regard, however, several factors must be considered. Although we do not know the depth from which water is being upwelled, it is most likely to be coming from near the top of the thermocline, where the temperatures are not strikingly low (Figure 15). A further complication is the possible return flow along the top of the thermocline towards the equator suggested by Fofonoff and Montgomery (1955). This mechanism could return water that has converged north of the equator to the undercurrent, where it might be enriched and re-upwelled. Thus, even rapid north-south circulation and upwelling at the equator do not necessarily call for intense cooling at the equator.

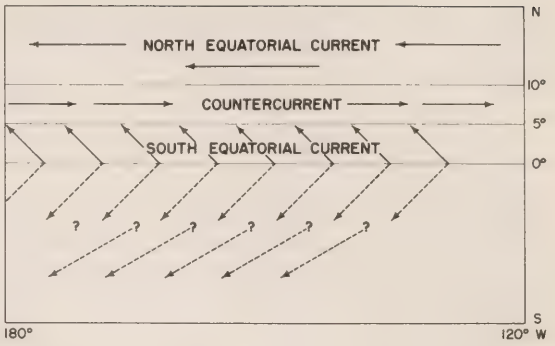

FIGURE 19.—Schematic view of the equatorial current system incorporating recent empirical determinations of flow north of the equator. Flow south of the equator is indicated as questionable.

These arguments show that the circulation between the equator and the Countercurrent is exceedingly complex and as yet imperfectly known. There is, however, enough evidence to suggest that the region between long 120°W and 180° is not a single east-west system with respect to identity or homogeneity of origin of its water. The available evidence indicates that it should be regarded as a series of adjacent homologous northwesterly flowing circulation cells (Figure 19). As will be demonstrated, the distribution of properties, e.g., nutrients, plankton, and fish,

is more readily reconcilable with this concept than with the classical flow pattern depicted in Figure 5.

Geographical Variation

We have advanced the concept that the flow pattern in the northern latitudes of the equatorial waters consists of a series of homologous northwesterly flowing cells. A study of the distribution of physical and biological properties, e.g., winds, water temperature, nutrients, plankton, and fish, indicates that they are more readily reconcilable with the homologous cell concept than with the classical flow pattern depicted in Figure 5.

Winds.—The wind system is the source of energy for the equatorial circulation, and it is logical to approach the problem of geographical variation of tuna by first examining the variations in the winds. The average distribution of winds (Figure 20) clearly shows a peak of wind stress near long 130°W, and in this area the equator is dominated by the southeast trades. Farther west the two trade systems are about equally distributed and the average force declines. In the far west the northeast trades dominate and the average force is low.

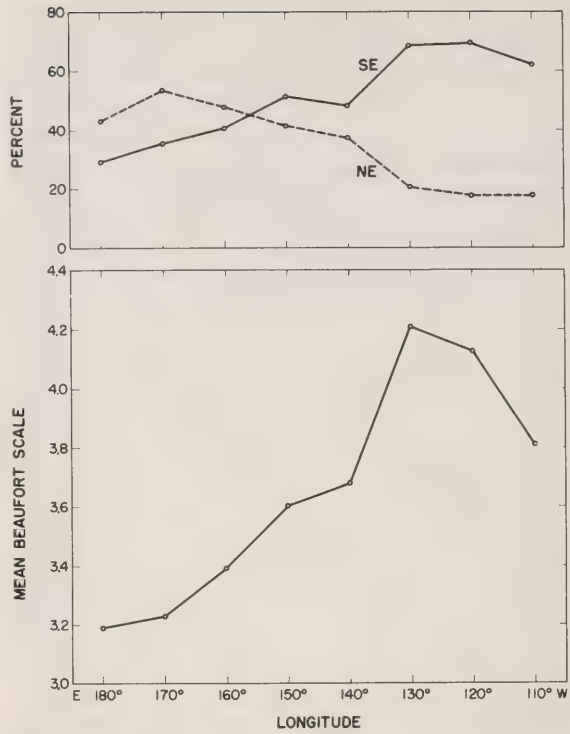

FIGURE 20.—Average direction and force of winds over the equator. The values were derived from U.S. pilot charts for 1953. In arriving at a value for a given longitude we averaged the winds in the four 5° squares focusing on the intersection of the meridian and the equator. East winds were apportioned equally between northeast and southeast.

Water temperature.—If the wind is the causal force behind the upwelling and poleward displacement of enriched (cooled) water, there should be a demonstrable relation between variation in the mean wind and variation in the mean water temperature. Table 2 depicts the mean monthly temperature of the surface waters north of the equator. It clearly shows the general trend to warmer water in the west in the zone between the equator and lat 5°N, which is the expected result of the wind gradient (Figure 21).

More significant is the variation in the size of the water temperature gradient from east to west. For instance, during March there is practically no slope but during October there is a steep slope (Table 2). The size of these gradients, when plotted against a measure of the gradient of southeasterly winds (Figure 21), suggests a causal relationship. When the wind gradient is large the gradient in water temperature is steep, and vice versa. We can now proceed with confidence on the assumption that variations in the winds are responsible for variations in water temperature through altering the rates of upwelling and the northward displacement of cool water.

Nutrients.—It is now in order to examine the distribution of nutrient salts in the euphotic zone along the equator to see whether the concentration varies with the amount of upwelling as evidenced by winds and water temperature.

TABLE 2.—Mean surface temperatures by longitudes and months for lat 0° to 5°N (basic data from U.S. Weather Bureau, 1938).

Month	Longitude west						
	110°	120°	130°	140°	150°	160°	170°
January	24.9	25.7	25.0	25.7	26.3	26.7	27.2
February	25.6	25.6	25.7	26.2	26.1	26.2	27.0
March	26.6	26.2	25.9	26.7	26.8	26.7	26.7
April	26.8	27.1	26.4	26.6	26.9	26.9	27.2
May	27.1	26.9	26.4	26.8	27.1	27.1	28.0
June	26.1	25.9	26.8	27.7	27.6	27.5	27.9
July	25.1	25.6	25.9	26.6	26.9	27.3	27.5
August	24.6	25.1	25.6	26.0	26.7	27.1	27.7
September	24.6	24.6	24.9	26.0	26.7	27.2	27.8
October	24.4	24.6	25.3	25.9	26.9	27.3	27.7
November	24.9	25.1	24.9	26.0	26.7	27.3	27.3
December	24.9	25.1	25.1	25.2	26.1	26.4	27.3
Mean	25.4	25.6	25.7	26.3	26.7	27.0	27.4

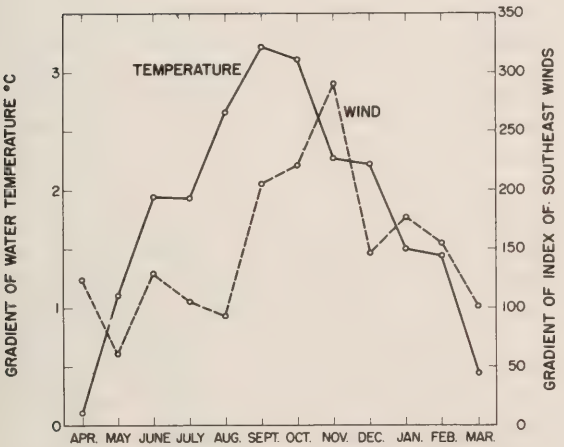

FIGURE 21.—Gradients of mean surface water temperature, equator to lat 5°N, and stress of southeast winds across the equator between long 120° and 170°W. We prepared the index of southeast wind stress by multiplying the percentage occurrence by the average force. The basic data are from the four wind roses that focus on the intersection of the equator and the appropriate longitude in the U.S. pilot charts for 1953. Half of the due east winds were arbitrarily assigned to the southeast quadrant.

Because of the lack of measurements of other salts, we will consider only inorganic phosphate. Even a discussion limited to this property must be considered poorly documented, however, because of the few measurements and the inherently erratic nature of phosphate determinations.

In considering the distribution of phosphate, we have constructed several temperature-phosphate curves from along the equator (Figure 22). We elected to use the temperature-phosphate curve because it seemed to yield the best available index of enrichment. Although low temperatures appear to be a good index of upwelling and relative enrichment when a single meridional section is being considered, it does not necessarily follow that relative coolness among meridians along the equator is a good index of enrichment, for there are marked east-west gradients in such factors as the depth of the thermocline (Austin, 1958). Temperature-phosphate curves should permit evaluation of the differences associated with these gradients and should indicate the "enrichment potential" along the equator.

The surface temperature relations among the temperature-phosphate curves in Figure 22 are consistent with the general east-west distribution of temperature, i.e., cooler water to the east suggests that they represent typical rather than atypical conditions. Phosphate, however, does not follow temperature when the several longitudes are considered together. Inorganic phosphate is lowest along long 117°W, where the surface water is coldest, and highest along long 140°W, where water temperature is intermediate. These differences in the basic temperature-phosphate relation appear to persist to rather low temperatures and therefore to considerable depths.

We will not attempt to explain the differences

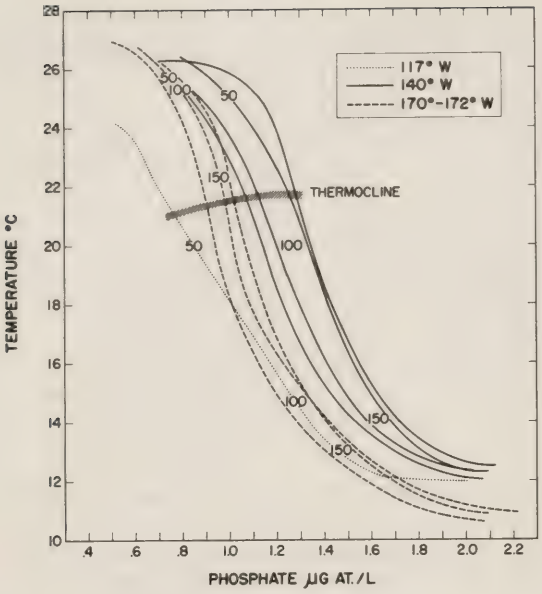

FIGURE 22.—Temperature-phosphate curves from the equator at several longitudes. The thermocline approximately corresponds with the 21°C isotherm. The approximate depth in meters for each group of curves is shown. Where one longitude is represented by several curves, the stations are separated in time from several weeks to several months.

in the distribution of phosphate. Accepting the differences among longitudes (Figure 22) as valid, it is clear that, though inequality in wind stress might be directly related to the amount of upwelling and consequently of cooling of the euphotic zone (as appears to be the case), these inequalities in wind stress will not necessarily be directly related to variations in the amount of enrichment. A given wind stress will probably produce the most enrichment along long 140°W, whether the energy is chiefly dissipated in the region of the thermocline or is dissipated uniformly with depth. The difference, however, will be most striking if the principal effect of the wind is expended in disturbing the thermocline. For instance, water diffused up from the thermocline along long 140°W will contain nearly twice the amount of nutrient salts as water diffused up from the thermocline at long 117°W.

Considering the variations in the vertical distribution of nutrient salts (Figure 22) and the geographical distribution of wind stress (Figure 20), it appears that on the average the greatest enrichment might be in the center of the system (near long 140°W), for in this region wind stress is high and the thermocline is abundantly supplied with nutrients. To the west, enrichment could very well fall off, since the wind stress declines, and to the east, enrichment might decrease because the thermocline is impoverished.

The discussion above is admittedly based on scanty and perhaps unreliable data. The general conclusion—that we should expect the most enrichment near the center of the area under consideration—is, however, compatible with the biological data to be considered next. Even more important, the phosphate-temperature curves indicate an east-west heterogeneity in the distribution of physical and chemical properties. This heterogeneity is consistent with the model of flow pattern (Figure 19) evolved from longline drift data.

Biological properties.—The biological properties along a latitudinal axis (Figure 23B, C) do not follow the temperature gradient (Figure 23A and Table 2) but rather tend to be distributed in conformance with the general enrichment pattern described in the previous section on nutrients. Both plankton and yellowfin tuna tend to be highest in the center of the region, where the measurements suggest enrichment is greatest.

The plankton distribution (Figure 23B) is somewhat unreliable to the east of long 150°W because the samples are few and unequally distributed in time (King, 1954; King and Hida, 1957). Nevertheless, all evidence points to a peak of plankton coinciding with or slightly west of the peak in enrichment.

The distribution of yellowfin tuna (Figure 23C) is more orderly than that of zooplankton, possibly because of a more orderly temporal and spatial stratification of the samples. The peak abundance of tuna is close to the longitude of maximum enrichment and the longitude of maximum standing crop of zooplankton.

Though there is general agreement between the standing crop of zooplankton and tuna, there are several discrepancies. For instance, the

high in zooplankton volume is only about 50% greater than the low, whereas for yellowfin tuna this difference is about 300%. These facts could indicate the inadequacy of some of the implicit assumptions, such as the standing crop of zooplankton is a measure of the standing crop of tuna forage, and the latter is a measure of the abundance of tuna; the longline catches are a measure of the abundance of yellowfin tuna; the abundance of yellowfin tuna is representative of its trophic level; and the system is equally efficient at all levels. Nevertheless, the general correspondence of the peak of zooplankton and yellowfin tuna appears more than casual (King and Hida, 1957).

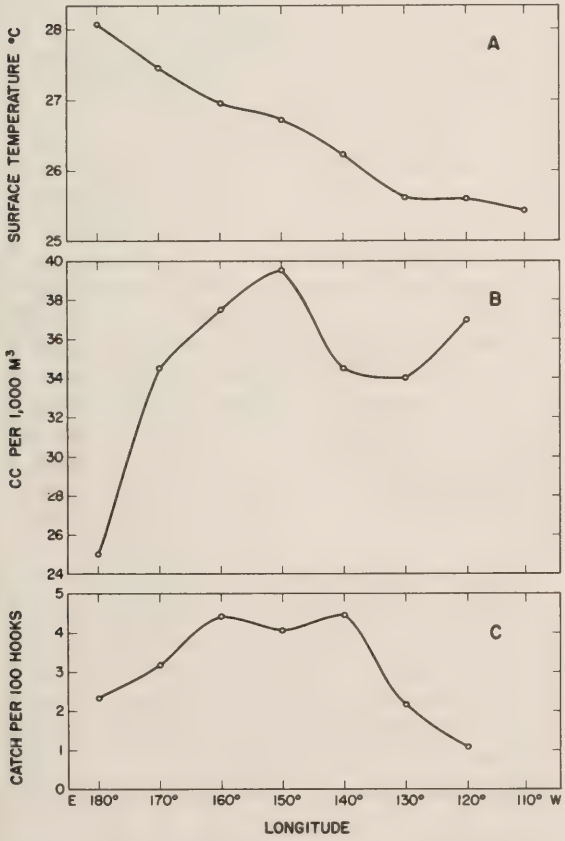

FIGURE 23.—A. Mean surface temperature from the equator to lat 5°N (U.S. Weather Bureau, 1938). B. Mean zooplankton from lat 5°N to lat 5°S (King and Hida, 1957). C. Mean yellowfin tuna catch from lat 5°N to lat 5°S.

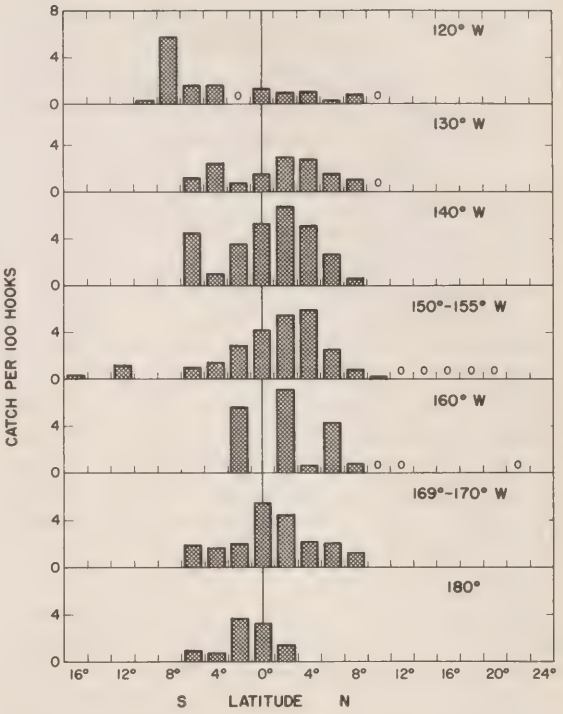

FIGURE 24.—Mean distribution of deep-swimming tuna. (The zero figures in the panels represent fishing effort expended, but no catches made; all stations 96.5 km or more miles from land.)

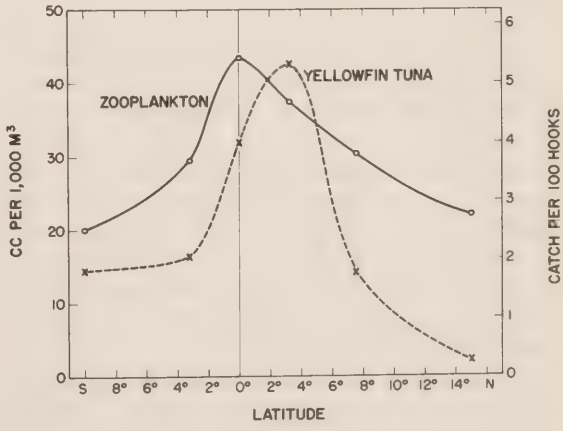

FIGURE 25.—Relative north-south displacement of zooplankton and yellowfin tuna. (Adapted from King and Hida, 1957.)

Associated with the longitudinal variations in average catch rates, the distribution of yellowfin tuna on a meridional plane appears to differ with latitude (Figure 24). In the extreme east (long 120°W), where enrichment is low, abundance of yellowfin tuna is also low and there is little evidence of increased abundance associated with the equator. Farther west (long 130°W) the abundance of yellowfin tuna is higher, and the expected peaking under prevailing southeast trades appears north of the equator. In the center (about long 150°W), where enrichment is thought to be highest and southeast trades predominate, abundance is high and centered well north of the equator. In the west, where enrichment is low and northeast trades are predominant, abundance of these tuna falls off and their distribution center is at or slightly south of the equator.

Discussion.—The available physical measurements, e.g., drogue movements and longline drifts, suggest that the northward movement from the equator is of considerable importance relative to the westward motion, and this conclusion is at variance with the results, based on ship's logs, depicted on either pilot charts or other summaries, such as our Figure 5.

As discussed in earlier sections, northward displacement of tuna with respect to plankton (Figure 25) is attributed to the time lag in the development of tuna forage, for during this period the waters are moving in a northerly direction. This northward displacement appears perfectly logical, but if so, and if the westerly flow is greater than the northerly flow, as we have generally assumed, the peak of tuna abundance should be displaced well tc the west of the zooplankton peak.

The available data (Figure 23) give little or no evidence of westerly displacement of the tuna peak relative to the zooplankton peak. This observation, coupled with empirical measurements showing that the northerly component of flow is vigorous and that the phosphate distribution is heterogeneous, makes it difficult to accept the earlier concept of an overriding western element of flow. The model, elaborated in the previous sections, that is consonant with all the evidence regards this portion of the South Equatorial Current from the equator to lat 5°N and long 120°W to 180° as comprising a series of homologous, parallel, northwesterly transport systems (Figure 19).

Temporal Variation

Variations in enrichment and distance from the source of enrichment were advanced as explanations for north-south and east-west variations in the abundance of yellowfin tuna in the region north of the equator. Most of the north-south distributions were readily reconcilable with temperature, phosphate, and plankton fields. The east-west distributions can also be explained in the same general terms, but the arguments are somewhat weaker, because the sampling program gave first priority to elucidating the distribution along the north-south axis. As a final step we propose to show that even the temporal variations in yellowfin tuna can be explained within the same framework as the spatial variation.

Murphy and Shomura (1953b) pointed out that during seasons or in areas dominated by the southeast trades yellowfin tuna tend to be concentrated north of the equator and that during periods of variable or northeast winds they tend to straddle the equator (Figure 26). This finding is consistent with the hypothesis, because either light, variable, or northeast winds should reduce the northward motion of water from the equator.

Averages such as those in Figure 26 may be misleading simply because the sampling has not been well stratified. Furthermore, although there are climatological seasons along the equator, they may frequently be altered or obscured by short-term changes to the extent that during a given year the "seasons" may not materialize. Because of the few meteorological observations in the area under consideration, it is difficult to evaluate the years in which we fished in terms of the normal. For these reasons, we evaluate the temporal changes in fish catch along a meridian in terms of the environment prevailing at the time of the catches, thus overcoming the lack

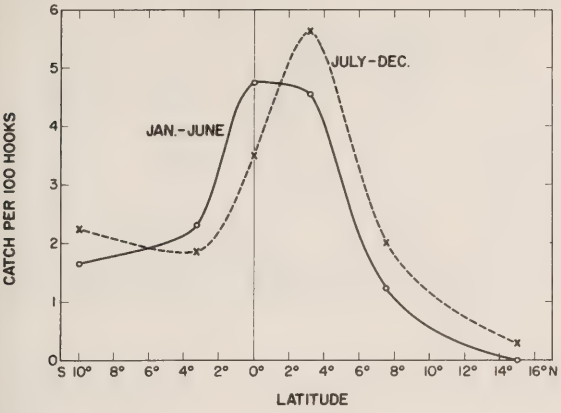

FIGURE 26.—Variation in yellowfin tuna catch with the current system for the two 6-month periods, January-June, a period with northeasterly or light and variable winds, and July-December, a period of prevailing southeasterly winds (in the equatorial central Pacific). (Adapted from King and Hida, 1957.)

of continuity of measurements of the fish and the environment.

To effect this type of analysis we must use some property in the environment that is consistently measured at each fishing station. Atmospheric data, such as winds and water temperature, are available. Winds are not suitable, because they are not conservative and because theory holds that there is a considerable lag between wind action and the response of the fish. Water temperature is more promising, since it is relatively conservative and is also a property of the immediate environment of the fish.[6]

In effect the study becomes limited to an analysis of variation along separate meridians or groups of adjacent meridians, because the water on widely spaced meridians is in all likelihood different with respect to origin and properties, such as the temperature-phosphate ratios. Furthermore, we have restricted the analyses to the zone north of the equator (lat 1°-5°N), where sampling was most intensive and where the theory of circulation is most advanced (Cromwell, 1953). The immediate vicinity of the equator is avoided on the basis of possible complications arising when this site of upwelling is considered and the unknown influence of the easterly flowing undercurrent.

Defining the geographical unit to be used in the time variation analysis as a single longitude or immediately adjacent longitudes between lat 1° and 5°N permits the development of a hypothesis. Wind action causes upwelling at the equator and a northward movement of upwelled water. This water, which might be termed "new," is cold, high in phosphate, high in plankton, and low in yellowfin tuna abundance. The meridional sections indicate that after it moves north, away from the possibility of further enrichment, it warms; phosphate declines, presumably from use; zooplankton declines, presumably from grazing; and yellowfin tuna abundance increases, presumably because the tunas congregate to feed on the forage organisms responsible for the decline in zooplankton. Water that has reached this final stage can be termed "mature."

This same reasoning can be applied to temporal variation in water temperature in places removed from the site of upwelling, i.e., the zone between lat 1° and 5°N. In this zone, the presence of cooler water must mean that the wind-driven northward movement was or is more vigorous and that the water there has been more recently enriched and has been in the euphotic zone for a shorter period of time. Consequently, it should contain more phosphate, more plankton, and fewer yellowfin tuna. Warmer water must have been longer in the euphotic zone, perhaps the result of a slowing of the wind circulation, and should contain less phosphate, less plankton, and more yellowfin tuna.

Phosphate.—If the hypothesis outlined above is correct, the concentration of phosphate in the ocean water north of the equator should be less in warmer water than in colder water, without regard to the time of sampling or place of sampling, providing consideration is restricted to the zone between upwelling and the Countercurrent

[6] It might be argued that surface temperature does not represent any substantial body of water. Fortunately, in the zone north of the equator the surface temperature is generally representative of the entire mixed layer, providing the effect of diurnal heating is suppressed. This has been done by using temperatures measured at about 9 m below the surface.

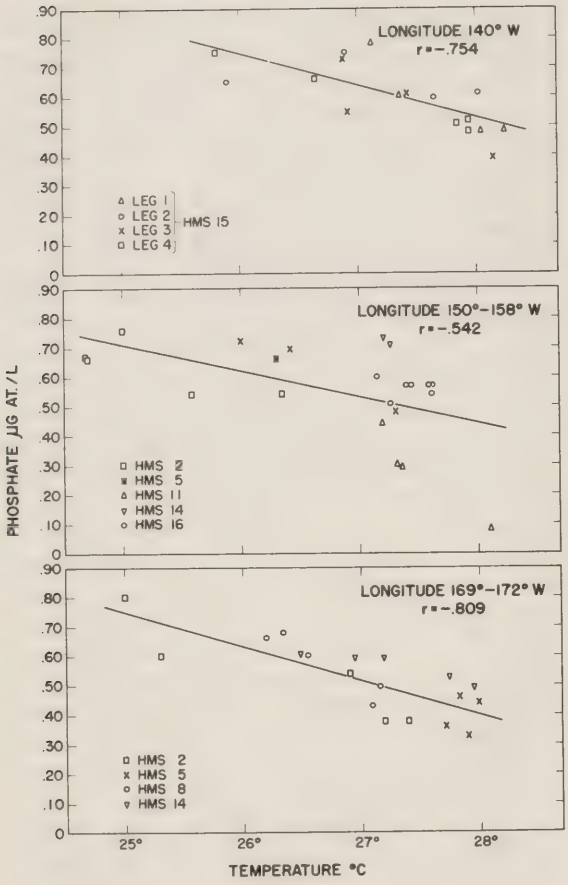

FIGURE 27.—Relations between temperatures and inorganic phosphate between lat 1° and 5°N.

and also providing single or closely adjacent longitudes are considered.

Unfortunately, there is not enough material available for a rigorous examination of surface temperature-phosphate ratios. The available data (Figure 27) between lat 1° and 5°N behave in a manner consistent with the hypothesis. Along each longitude is the expected negative regression with respect to temperature. The heterogeneity among longitudes is indicated by the reduced value of r (Table 3) when all data are considered together.

Zooplankton.—The relation between temperature and zooplankton should theoretically be a curve skewed to the right, for time should elapse between enrichment and peaking of the copepods that form the bulk of the catches. We already know, however, that the peak of zooplankton is coincident or nearly so with the center of upwelling, and since we have restricted ourselves to the zone north of the upwelling (lat 1°-5°N), we should expect to find only the descending limb of the curve.

TABLE 3.—Relation of temperature to phosphate in the zone of lat 1° to 5°N[1].

Longitude	Number of sections	Number of paired observations	Correlation coefficient (r)	Probability
140°W	4	17	—0.754	<0.01
150°-158°W	5	22	—0.542	<0.01
169°-172°W	4	19	—0.809	<0.01
180°	1	5	—0.833	>0.05
All observations	14	63	—0.377	<0.01

[1] Data from Cromwell (1954), Austin (1954a, b), and Stroup (1954). Each temperature and phosphate measurement is from the Nansen bottle immediately below the surface bottle, generally at about 10 m.

The plots in Figure 28 indicate a significant negative relation between temperature and zooplankton, though the relation is not as striking as that between temperature and phosphate. Some of the variability may be attributable to sampling errors and some to systematic errors, such as day-night variation. As in the instance or the phosphate, the values of the correlation coefficients are higher (except for long 140°W) for the individual sections than for the data as a whole (—0.472, —0.718, —0.679 versus —0.567 for all data).

Yellowfin tuna.—We have shown that maturity of the water, as indicated by the temperature of the mixed layer, appears significantly related to the amount of dissolved nutrients (phosphate) and the amount of zooplankton. It remains to project this reasoning up the trophic levels to yellowfin tuna. Probably one or more trophic levels must intervene between the zooplankton sampled and tuna, for King and Demond (1953) showed the zooplankton to be mainly copepods, and Reintjes and King (1953) showed that, although yellowfin tuna consume a variety of organisms, the bulk of their diet is composed of squid and fish.

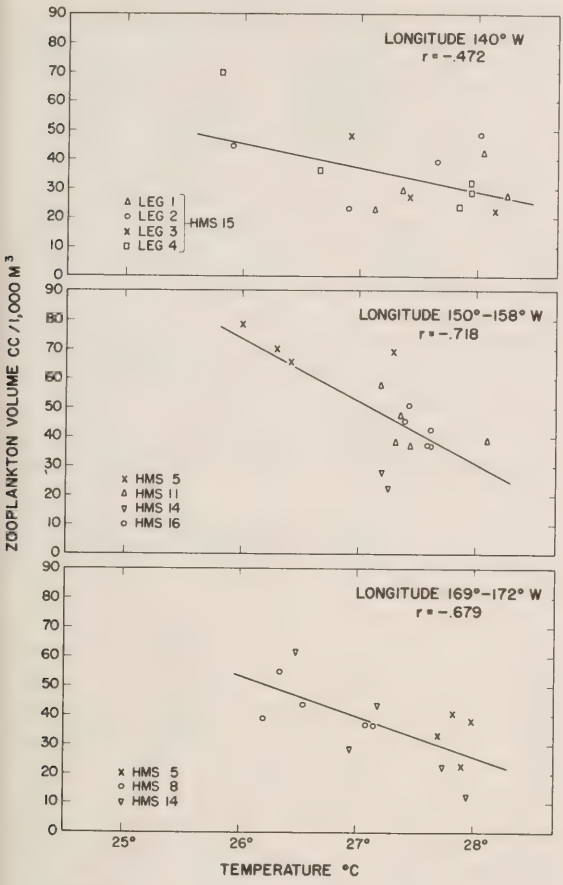

FIGURE 28.—Relation between temperature and zooplankton abundance between lat 1° and 5°N.

In attempting to specify the expected relation between yellowfin tuna and water maturity (temperature), it is helpful to start with the tuna and work back through the trophic levels. The tuna are highly motile and are capable of concentrating where food is most abundant. That is, they are not restricted to development in situ in a mass of water. To a lesser extent some of their food organisms (the larger squid and fishes) are undoubtedly able to concentrate in favorable areas that they discover either by following gradients or by random movements. It seems extremely unlikely, on the other hand, that the members of the next lower trophic level (organisms that feed on the small zooplankton) are capable of long migrations.

If this intermediate link is incapable of migration, it must develop in situ; it must be, at least indirectly, responsible for grazing down the "net zooplankton" which we measure, and because of the time needed for growth, it must reach a climax at some time after the zooplankton. Thus, we expect the forage for tuna to keep improving for some time after the zooplankton has reached its maximum development.

Since the water is warming during this period, there should be a positive relation between temperature and yellowfin tuna abundance until the water reaches senescence, at which point further increases in temperature should be accompanied by a decline in yellowfin tuna abundance. It appears, however, that actual senescence is never attained, at least in the portion of the system under study (long 120°-170°W). Instead, water probably is withdrawn from the system through convergence and possibly by the Countercurrent before reaching senescence, or even possibly before reaching maturity.

When fish catches are plotted against temperature (Figure 29), a striking relation is shown between maturity of the water (as measured by temperature) and abundance of yellowfin tuna. The measure of abundance of the tuna requires some explanation. As shown by Murphy and Elliott (1954), the catch at a single longline station is subject to very wide sampling errors—so wide in fact that any relations between catch and variables in the environment are likely to be poorly defined. For this reason the several catches in the zone of lat 1° to 5°N, during a single crossing, are considered as a unit. This treatment, in addition to suppressing sampling error, also has the advantage of directing attention to a zonal situation rather than to a point in the ocean, thereby eliminating the possible effect of other regressions along a meridional section. The temperature index parallels the tuna index in that it is also the average surface temperature over the lat 1° to 5°N zone.

Returning to the temperature-yellowfin tuna regressions, the steep slopes on long 120° and 130°W suggest a positive relation between maturity and catch. At long 148° to 155°W the

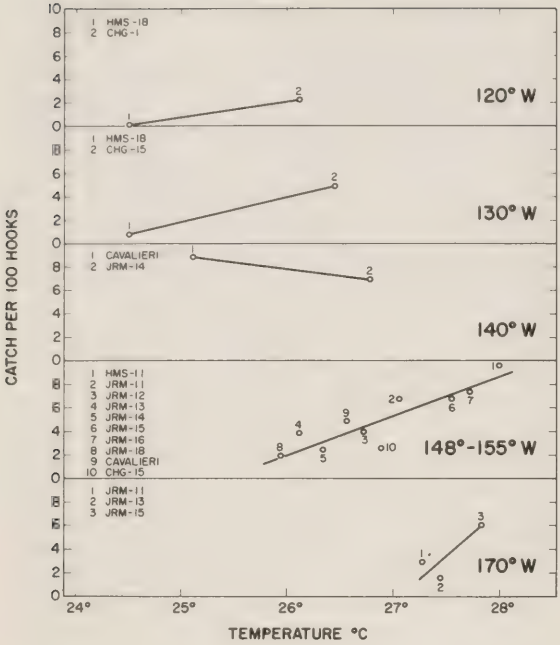

FIGURE 29.—Relations between yellowfin tuna catch and surface temperature at several longitudes for the zone lying between lat 1° and 5°N.

relation is striking and highly significant, and finally on long 170°W the positive relation is again suggested. Thus, with the exception of long 140°W, all of the fish catch data agree with the hypothesis that time variations can be explained in terms of the maturity of the water and that variations in the biota can be estimated by water temperature in this region.

The single exception (long 140°W) appears atypical in other respects. Good catches of tuna were obtained in relatively cool water, but the fishing evidently coincided with a time of rapid change; a few days after the good fishing the water cooled further and the fishing became poor. Thus, the good fishing occurred during a change from environmental conditions associated with good fishing to those associated with poor fishing. During such transitions we might expect irregularities in the relation between water maturity and catch.

The fish catches and temperatures at long 148° to 155°W plotted against time from 1951 to 1954

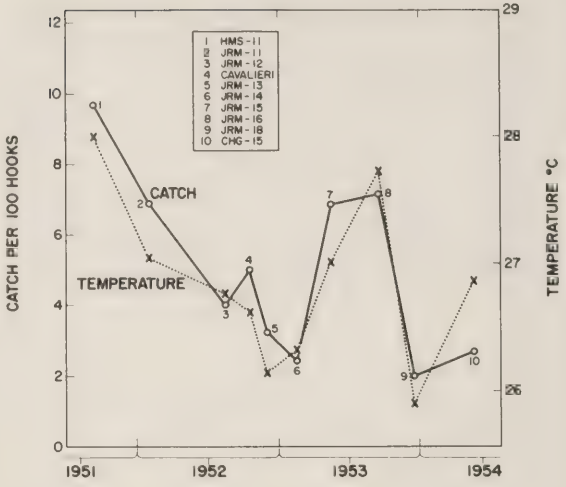

FIGURE 30.—Temperatures and fish catches between long 148° and 155°W plotted against time, 1951-54.

(Figure 30) reveal the basic relation shown in Figure 29. Generally cooler water and poorer fishing are indicated, however, in 1951-54. Superimposed on this trend is a suggestion of rising temperatures during the first half of each year and falling temperatures during the second half. These bear some resemblance to the average trends given in Table 2, but, insofar as these data are adequate, a long-term trend to cooler water appears to have almost completely suppressed the seasonal trend during 1952, thus pointing up the difficulties attending "seasonal analysis" in the equatorial area.

Temperature profiles.—It is instructive to examine the shape of the several meridional surface temperature profiles at long 148° to 155°W, because the average temperature that was compared with yellowfin tuna abundance tends to obscure certain important features. The several profiles in Figure 31 suggest that a variety of situations exists.

Two of the profiles (panel A) show relatively cool water from the equator to at least lat 4°N. This "flat" feature at low temperatures suggests very active upwelling and a northward displacement of immature water; therefore, it is not surprising that these two transects are associ-

ated with the lowest catch rates shown in Figures 29 and 30.

A second group of three profiles (panel B) has in common cool water at the equator and a steep gradient rising from south to north. This steepness of the gradients also suggests active upwelling and northward movement, and the average low water temperature implies the presence of immature water. Like the two profiles shown in panel A, these three are also associated with poor catch rates.

The profiles in the last group (panel C) show relatively little gradient, at least from lat 1.5° to 5°N. Such "flat" profiles at high temperatures should arise if upwelling and northward movement of water has slowed down, possibly in response to a shift from southeast to northeast winds or simply a marked decline in wind force. The four high catch rates shown in Figures 29 and 30 were obtained during these four periods.

The nature of the sequence of events leading to a relatively high abundance of yellowfin tuna can be inferred from the temperature profiles. First a body of enriched water should be created, and this body of water should be permitted to mature relatively undisturbed; that is, the north-south system should be slowed down. The distribution of the winds (Figure 20) suggests that such a sequence of events is most apt to occur in the central portion of the area (long 140°-160°W). In the east, southeast trades of high velocity persist during most of the year, possibly creating a south-to-north circulation with attendant convergence of such vigor that the water rarely matures in terms of tuna forage production. In the center, the southeast trades still have the substantial velocity needed to induce upwelling, but their frequency is only about 50%, suggesting there is frequently an opportunity for the water to mature. In the far west, neither

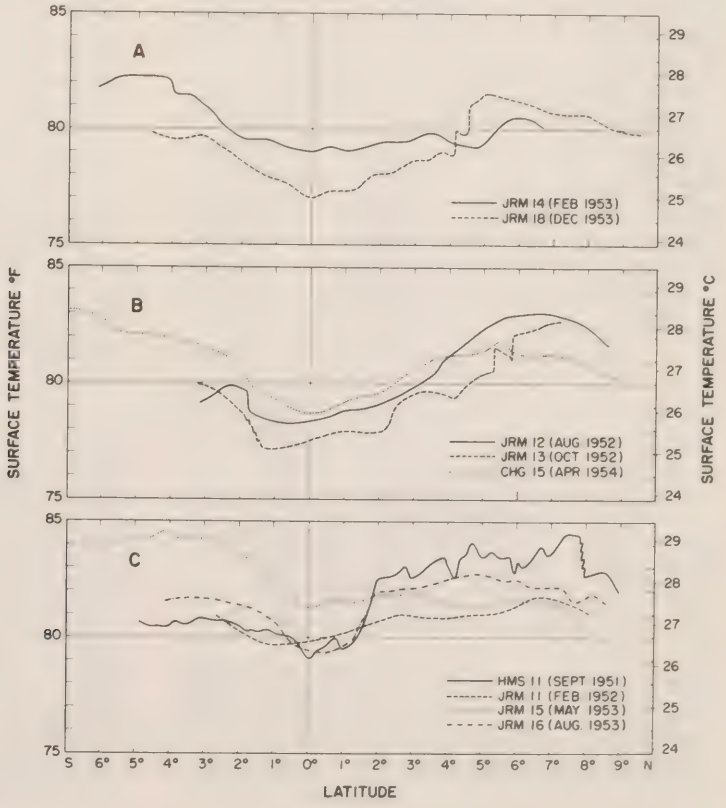

FIGURE 31.—Surface temperature profiles on longline fishing cruises along long 148° to 155°W. A. Low temperatures between lat 1° and 5°N. B. Low temperatures and a steep north-south gradient between lat 1° and 5°N. High temperatures between lat 1.5° and 5°N.

the velocity nor the frequency of the southeast trades appear high enough to create substantial bodies of enriched water north of the equator.

We now have two processes that might account for poor yellowfin tuna fishing in the east and west and good fishing in the center. The one, involving the wind pattern just described, rests on the assumption that if enriched water is to result in a dense population of yellowfin tuna, it must remain relatively undisturbed in the euphotic zone long enough for a forage population to develop. The other, discussed in the section on nutrients, is based on the vertical distribution of phosphate at various longitudes along the equator. Phosphate distribution, when viewed against the wind distribution, suggests that the absolute amount of enrichment might be greatest in the center of the area, and it is in this area that the enriched water appears to have a reasonable chance to mature before convergence. The two processes are independent but interact in a way consistent with the occurrence of the best yellowfin tuna fishing in time and space.

In addition to variation in the catch rates at a given longitude, there have been changes in the meridian of the best catches. For the year 1953 there are enough records to illustrate this phenomenon (Figure 32). Such shifts are in harmony with the present theories of the factors controlling yellowfin tuna abundance. The yellowfin tuna are highly motile, and we expect them to be most abundant where conditions best suit them. For instance, if upwelling is too vigorous over the area from long 120° to 150°W and less vigorous farther west, conditions should be better in the west. This situation may well explain the pattern in May-June of 1953 (Figure 32). On the other hand, in August 1953 yellowfin tuna seemed to be most abundant near long 155°W; this distribution would be expected if strong upwelling and northward displacement at some time in the past was followed by a period of relative quiet.

These deductions are difficult to test critically, i.e., it is difficult to make a critical comparison between fish catch and some factor in the environment such as temperature because of the heterogeneity of the water when considering the equator as a whole. However, there is a suggestion of an association in our data: During February-April 1953 (Figure 32) the catch was better on long 140°W than on long 150°W, and at the same time the mixed layer was about 0.5°C lower on long 150°W than on long 140°W. This is a reversal of the average trend (Figure 23) and could only have resulted from the water at long 150°W being more recently affected by upwelling and northward displacement than that at long 140°W. In perfect agreement with our hypothesis, this relatively newer water at long 150°W had a smaller population of tuna.

In summary, it has been possible to develop a functional hypothesis consonant with the mechanics of the equatorial system that can logically account for all, or nearly all, of the major observed variations in the abundance of the large deep-swimming yellowfin tuna. The theory successfully embraces variations in catch rate in respect to time and in respect to space. Since the root of the system lies in the winds, it should be possible eventually to anticipate the variations in the yellowfin tuna population by examining variations in the wind regime.

SURFACE TUNAS

The principal methods we have used to sample surface tunas are surface scouting and trolling. Live-bait fishing has also been used occasionally. These are the same methods used to locate tunas by the several live-bait and purse-seine fisheries in the Pacific.

Each of these survey methods has inherent weaknesses that cannot be estimated quantitatively. Perhaps the greatest difficulty in surface sighting lies in the state of the sea. The central Pacific is nearly always choppy, practically precluding detection of schools at the surface unless they are breaking water or are accompanied by feeding birds, e.g., in our experience 85% of all schools were first sighted through the accompanying "working birds." In effect, we do not see tuna unless their presence is marked by birds; this relation casts doubt on the census method. The problem, however, may not be as serious as it seems, for the association between birds

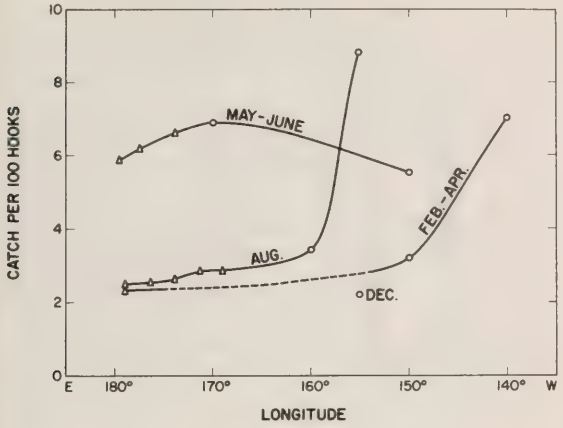

FIGURE 32.—Catch rates of yellowfin tuna by longitude and by time of year (1953).

and fish may have a firm biological basis in that feeding tunas, by driving small fish and squid to the surface, appear to be an important factor in making food available to birds.

The observed behavior of working bird flocks substantiates this contention. A bird flock may be first seen when it is feeding over a school, the birds excitedly circling close to the sea surface and frequently plummeting into the sea to capture prey. Subsequently, the school may sound and the birds discontinue feeding, scatter somewhat, and rise to a higher elevation as though scouting for the school. As soon as the school appears again at the surface, the birds quickly assemble over it and resume feeding. This relationship suggests that the abundance of pelagic predators such as tuna may directly affect the abundance of birds by controlling the amount of food available to them. Insofar as this is true, bird abundance should form an index of fish abundance.

On the other hand, it is difficult to discount completely the possibility of introducing error through the use of birds as an indicator of fish, for the frequency of sightings of both birds and fish is everywhere parallel (Murphy and Ikehara, 1955), and it seems unlikely a priori that the populations of both need always be parallel. For instance, birds and fish are seen more frequently around islands than far at sea. Oceanic birds nest on land, thus tending to make islands focal points for their populations; but, is the vicinity of land also a focal point for tuna schools? Perhaps so, for nesting birds have an even greater demand for food than wandering birds, and thus the magnitude of their concentrations around islands must be based on the food supply too and, to the extent that they obtain their food over schooling tunas, on the abundance of schools of surface tunas.

Aside from the problem of just what surface sightings mean in relation to tuna abundance, the validity of conclusions based on relatively scanty sampling of so vast an area as the central Pacific (Figure 3) can be questioned. The only available test, a comparison of sightings from the Laboratory's vessels with the seasonal changes in Hawaiian commercial landings (Figure 33), shows that in general a seasonal prediction based on our relatively scanty observations would have been borne out by the commercial catch. Thus, it appears that rather limited scanning of the sea can yield results compatible with those from a very large amount of effort (the commercial fishery).

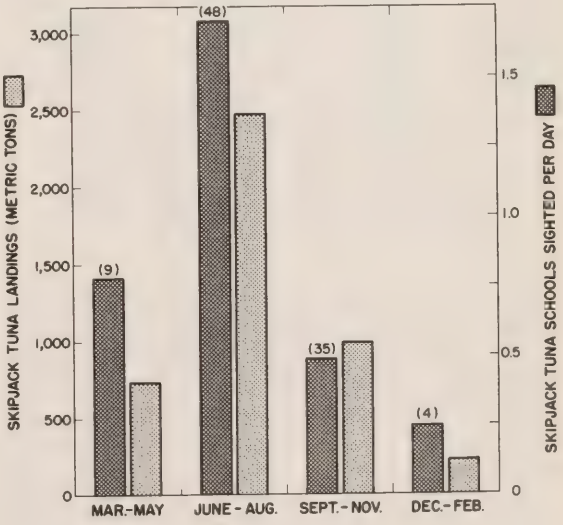

FIGURE 33.—Comparison between average Hawaiian skipjack tuna landings (1950-52) and surface sightings of skipjack tuna schools (number of schools sighted noted above bar diagrams) from research vessels in the Hawaiian Islands area (data from Murphy and Ikehara, 1955).

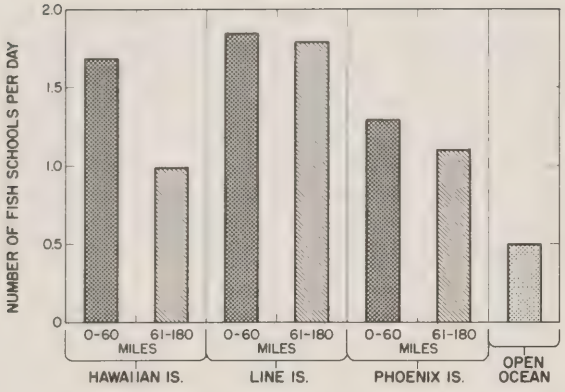

FIGURE 34.—Frequency of sighting fish schools in various zones (distance from land) and areas of the central Pacific (data from Murphy and Ikehara, 1955).

Systematic trolling is a well-known and established method of quantitatively surveying the availability of surface fish. The only serious flaw in our data has been the difference in availability to troll lures of the principal surface species, skipjack and yellowfin tunas (Murphy and Ikehara, 1955). For instance, near the Hawaiian Islands half as many yellowfin tuna were taken by trolling as skipjack tuna, whereas other measures, e.g., the commercial catch (June, 1951), suggest that there are only about one-tenth as many yellowfin tuna as skipjack tuna.

DISTRIBUTION OF SURFACE TUNAS RELATIVE TO LAND

The general abundance of surface schools depicted in Figure 34 shows that schools are seen several times more frequently near islands than in the open ocean. This can be interpreted as merely indicating the abundance of birds, but, as is shown later, it is also possible to regard the islands as creating in their vicinity special conditions that are conducive to the occurrence of surface-schooling tunas.

In addition to differences in abundance between island waters and the open ocean, species composition appears to shift, in that yellowfin tuna schools tend to favor the vicinity of islands (Figure 35). About 47% of all schools sighted

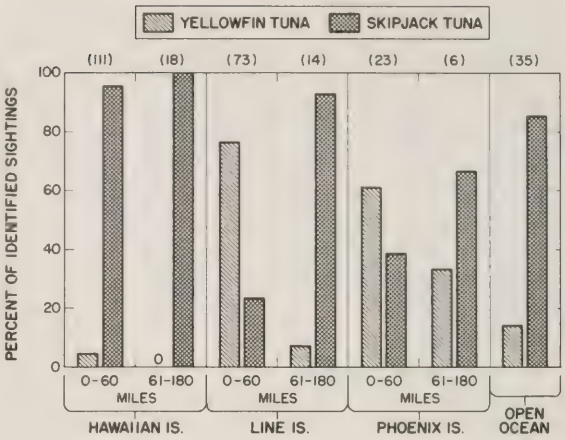

FIGURE 35.—Relative occurrence of yellowfin and skipjack tuna schools at various distances from land. Number above bar diagram represents total number of schools sighted.

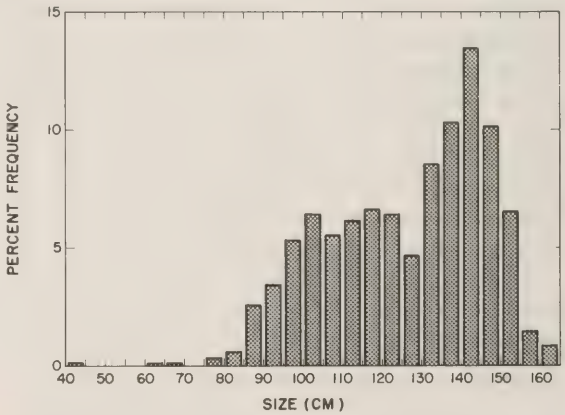

FIGURE 36.—Length frequency of longline-caught yellowfin tuna at all insular fishing stations (within 96.5 km of land).

were identified as either yellowfin tuna or skipjack tuna, a small percentage were identified as other species, e.g., the common dolphin, and the rest were unidentified (Murphy and Ikehara, 1955). The relative percentages of the two important species plotted in Figure 35 show very clearly that (1) skipjack tuna are dominant in the Hawaiian Islands area and in all offshore areas, and (2) in each instance relatively more

yellowfin tuna schools are found near land than offshore. In fact, in the Line and Phoenix groups yellowfin tuna appear to have replaced skipjack tuna near land. Thus the presence of land seems to create favorable circumstances for the occurrence of tuna schools in general and yellowfin tuna schools in particular.

This distribution of yellowfin tuna in relation to land is also borne out by longline catches of yellowfin tuna near land and offshore. Figure 36 shows that when longline gear is fished near islands it catches more of the smaller yellowfin tuna that compose surface schools than it does when fished offshore (compare Figure 36 with Figure 4). This increased abundance of small yellowfin tuna near islands is also shown in Figure 37, which indicates that about half of the increase in longline catch rates near shore stems from the addition of small fish to the catch. Furthermore, the increase in small fish in the longline catches is roughly proportional to the increase in the rate of surface sighting of this species near land. A final indication that small yellowfin tuna are more abundant near land is that surface trolling took 10 times as many yellowfin tuna per unit of effort within 96.5 km of land as beyond that limit (Murphy and Ikehara, 1955). Since all three sampling methods—longlining, sighting, and trolling—clearly show small surface yellowfin tuna to be more abundant near land, we conclude with little or no reservation that the occurrence of young yellowfin tuna in the central Pacific is intimately related to the presence of land.

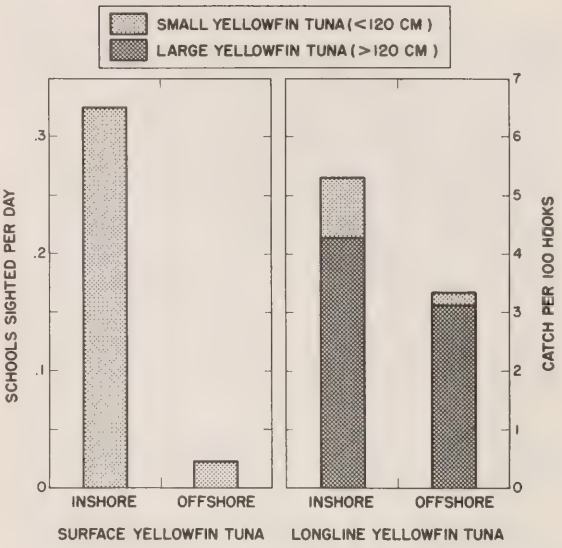

FIGURE 37.—Relative occurrence of schooling yellowfin tuna in surface sightings and longline catches for inshore and offshore areas.

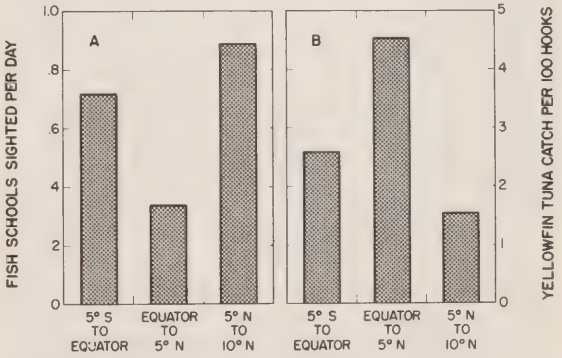

FIGURE 38.—Latitudinal distribution of surface tuna schools and deep-swimming yellowfin tuna. A. Sightings of surface tuna schools in the open ocean (Murphy and Ikehara, 1955). B. Yellowfin tuna catches from fishing stations more than 96.5 km from land and between long 140° and 170°W.

OCEANIC DISTRIBUTION

Despite the low average abundance of tuna schools in the open ocean (Figure 34) certain areas or zones appear to support populations with a density comparable to that of the island areas. Over most of the central Pacific our sampling is not adequate to focus attention on particular areas except in the central portion of the study area (long 140°-170°W). Here, there are enough days' observations to make meaningful zonal comparisons (Figure 38A). It is apparent that the number of schools sighted in some of these zones is nearly the same as for the Hawaiian Islands area, e.g., 0.9 school seen per day in the Countercurrent (Figure 38A, lat 5°-10°N) and 1.7 near the Hawaiian Islands (Figure 34). Considering how far removed these zones are from land, we might conjecture that considerably more schools would have been sighted if

more birds had been available. Such pelagic populations as these must represent a vast untapped resource, judging from the 5,000 tons or so taken annually in a limited area around the Hawaiian Islands (June, 1951).

The distribution of oceanic schools is at variance with the distribution of deep-swimming yellowfin tuna (Figure 38B), the most striking differences being the high density of schools in the Countercurrent (lat 5°-10°N) and south of the equator. In fact, the distribution of surface schools is almost the inverse of the distribution of deep-swimming tunas. This apparent inverse relation poses a serious problem, for a priori we would expect surface schools to respond to the equatorial enrichment in the same manner as the deep-swimming tunas.

The problem can be approached by considering the environmental factors that make it possible for an area to support large numbers of surface schools. The obvious one that comes to mind is the standing crop of forage, as indicated by zooplankton. We have already indicated, however, that zooplankton tends to peak at the equator (Figure 25), and thus food supply as indicated by the standing crop of zooplankton does not account for the north-south distribution of surface fish. In a possibly parallel situation, King and Hida (1954) found little or no more zooplankton around the Hawaiian Islands than in the North Pacific Current and were unable to account for the population of skipjack tuna around Hawaii on the basis of the standing crop of zooplankton.

A suggestion of an important environmental factor controlling the abundance of skipjack tuna was given by Robins (1952), who found a positive association between skipjack tuna troll catches and temperature discontinuities or "fronts." The circulation associated with fronts involves horizontal convergence and sinking, according to Cromwell (1956). This type of movement could act to concentrate organisms, particularly those that float or can actively resist sinking. Fronts might act as modifiers of the average standing crop by altering its distribution in space so that fishes can more effectively forage.

The effect of fronts on the distribution of forage might account for the abundance of schools near islands. An island mass in a moving ocean current must set up patterns of "frontlike" circulation cells and eddies, as has been shown for the Hawaiian Islands (McGary, 1955). These features, although perhaps not increasing the basic supply of food, should concentrate some of it so that fish can feed more efficiently.

In an effort to determine whether this same mechanism could be offered as an explanation of the irregular distribution of surface schools in the equatorial region (Figure 38), we determined the frequency of temperature irregularities at the sea surface, confining ourselves to the best-sampled zones, i.e., lat 5°S to 10°N, long 140° to 170°W. The frequency of occurrence of temperature irregularities or "fronts" was estimated from thermograph traces made while the ships were crossing the equatorial system in a north-south direction. An irregularity was simply defined as a temperature change that was completed during 15 min or less when the ships traveled at a speed of about 8 knots, i.e., long, even temperature clines were not considered. If the temperature rose (or fell) quickly to a new level, this was counted as one "front." If it both rose and fell during any interval, it was counted as two "fronts," providing the rise and the fall each took no more than 15 min.

An inquiry can logically be made into the relation of wind velocity to the number of such fronts, for on calm, hot days there may be many irregularities caused by convection currents set up by diurnal heating. A plot of wind force against the number of fronts in unit time, however (Figure 39), suggests that we are dealing with phenomena that are independent of the immediate wind stress and heating.

When we compare the rate of crossing fronts with the rate of sighting surface schools, we find a remarkable correspondence (Figure 40), enabling us to advance the same explanation for differences in abundance of surface schools among different areas of the open ocean and between the vicinity of islands and the open ocean. The responsible feature of the environment, the "front," meets the test of biological and physical logic, for temperature fronts are symptomatic of horizontal movement of water toward the dis-

continuity and sinking at the discontinuity, a mechanism that should concentrate certain types of tuna forage or food for tuna forage.

We are still confronted with the basic difference in the distribution of surface and deep-swimming tunas (Figure 38), though we have logically advanced two hypotheses that seem adequate to explain each distribution pattern when the problems are considered independently, i.e., basic enrichment and northward drift of upwelled water in the instance of the deep-swimming tunas, and "fronts" in the instance of surface schools. An entering wedge is offered by the difference in social behavior between the deep-swimming and surface schools.

Sette (1950), in discussing mackerel, proposed that schooling was advantageous to any predator feeding on prey that was aggregated. In fact, the very existence of schools of carnivores would seem to require schools or aggregations of prey, for if prey were distributed at random, it could be most effectively harvested by pursuit and capture of individuals by individual predators. In other words, where we find scattered prey we should expect scattered predators. In the present instance, where we have a mechanism ("fronts") for concentrating prey, we find surface schools, and where the mechanism is not present we do not find the schools. The deep-swimming tunas, on the other hand, are not aggregated into large, compact schools (Murphy and Elliott, 1954) and so might be expected to use more or less scattered forage organisms more efficiently, and the distribution of such tunas might be expected to conform more closely to the mean distribution of forage, rather than the distribution of concentrating mechanisms.

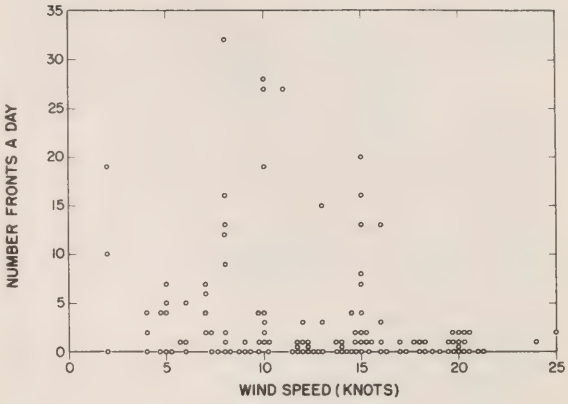

FIGURE 39.—Daily frequency of fronts as a function of daily noon wind speed (lat 5°S-10°N, long 148°-170°W).

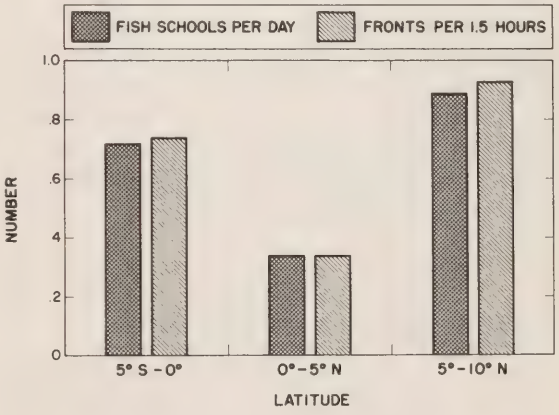

FIGURE 40.—Rate of crossing temperature discontinuities and rate of sighting fish schools near the equator (vessel speed about 8 knots, vessel course always north or south). Longitudinal limits 140° to 170°W.

SUMMARY

1. Surveys of tuna populations and environmental conditions were made in the equatorial central Pacific in 1950-53.

2. Tunas were sampled by longline, trolling, live-bait fishing, and sighting from the bridge of a research vessel.

3. The longline was used more than the other methods of fishing, because it was the most consistently productive sampling method, particularly on the high seas.

4. Tunas, especially yellowfin tuna, may be divided into two groups, small surface-swimming tunas and large deep-swimming tunas.

5. On the basis of longline catches, deep-swimming yellowfin in the central Pacific were most abundant near the equator.

6. Deep-swimming bigeye tuna were nowhere as abundant as yellowfin tuna. Two tongues of

relatively high bigeye tuna catches occurred in the equatorial Countercurrent.

7. Deep-swimming albacore were most abundant in the southwestern area, e.g., around lat 5°S, long 170°W.

8. Skipjack tuna were found over the entire area.

9. Deep-swimming yellowfin and bigeye tunas were larger in the east (e.g., 120°W) than in the west (e.g., 130°E). The reason for this difference is obscure.

10. Analyses of tuna catches and properties of the environment in a meridional plane revealed the following: There is upwelling and enrichment at the equator; the upwelled water is displaced northward; zooplankton peaks are at the center of upwelling, apparently because of a time lag in the development of tuna forage.

11. The water flow near the equator differs from the classical concept in that empirical measurements suggest the northward motion is of the same magnitude as the westward motion. Thus the South Equatorial Current just north of the equator should be regarded as a series of parallel, homologous, northwesterly flow systems.

12. Variation in surface temperatures at the equator is a function of surface winds, through alteration of the rate of upwelling.

13. Interaction of geographical variation in the vertical distribution of nutrient salts and the geographical distribution of wind stress cause the greatest enrichment through equatorial upwelling to occur in the central area (near long 140°W).

14. In the area surveyed, between long 120°W and 180°, both zooplankton and yellowfin tuna were most abundant near the center of the area (near long 150°W).

15. When northeast trades prevail, yellowfin tuna seem most abundant south of the equator; during southeast trades, north of the equator; and during variable winds, the peak abundance straddles the equator.

16. Between the equator and the Countercurrent the presence of colder water is associated with more phosphate, more zooplankton, and fewer yellowfin tuna. Warmer water is associated with less phosphate, less zooplankton, and more yellowfin tuna. We believe that these differences are a reflection of the time lapse since enrichment and that variations at a geographical locality are in response to variations in wind flow that affect the rate of upwelling.

17. There are suggestions of annual seasonal variations in the abundance of yellowfin tuna near the equator, but these may be masked by longer term secular trends.

18. Changes in abundance at a point on the ocean may result from east-west shifts in the yellowfin tuna population as well as north-south shifts, or simply general dispersion from or concentration at that point. All of these variations may be logically attributed to variations in the enrichment at the equator, brought about by variations in the winds.

19. Surface tunas are seen more often close to land, possibly because more birds are present there.

20. In the equatorial central Pacific, yellowfin tuna tend to predominate in surface schools close to land and skipjack tuna far from land.

21. Near the equator, the abundance of surface schools does not seem to coincide with the peaks in abundance of the deep-swimming tunas. Food concentrating mechanisms appear to be more important than basic food supply in affecting the local abundance of surface-swimming schools.

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We take great pleasure in acknowledging Oscar E. Sette for the leadership and guidance provided the authors during the investigation of the tuna resources of the equatorial central Pacific; the investigation upon which this report is based. As Area Director of the Hawaii Area from 1949 to 1955, O. E. Sette initiated this tuna-oceanography study of the vast unknown equatorial waters in 1949.

Practically the entire scientific staff of the former Bureau of Commercial Fisheries Biological Laboratory, Honolulu, helped collect the data at sea during the 1950-53 period. In the Laboratory, Jean S. Halling and Richard N. Uchida were responsible for much of the processing of biological data. In addition to O. E.

Sette, several other persons devoted thought and time to the formulation of the program. Chiefly, these are Donald L. McKernan, Thomas S. Austin, and the late Townsend Cromwell.

O. E. Kerns and Frank Williams reviewed the manuscript.

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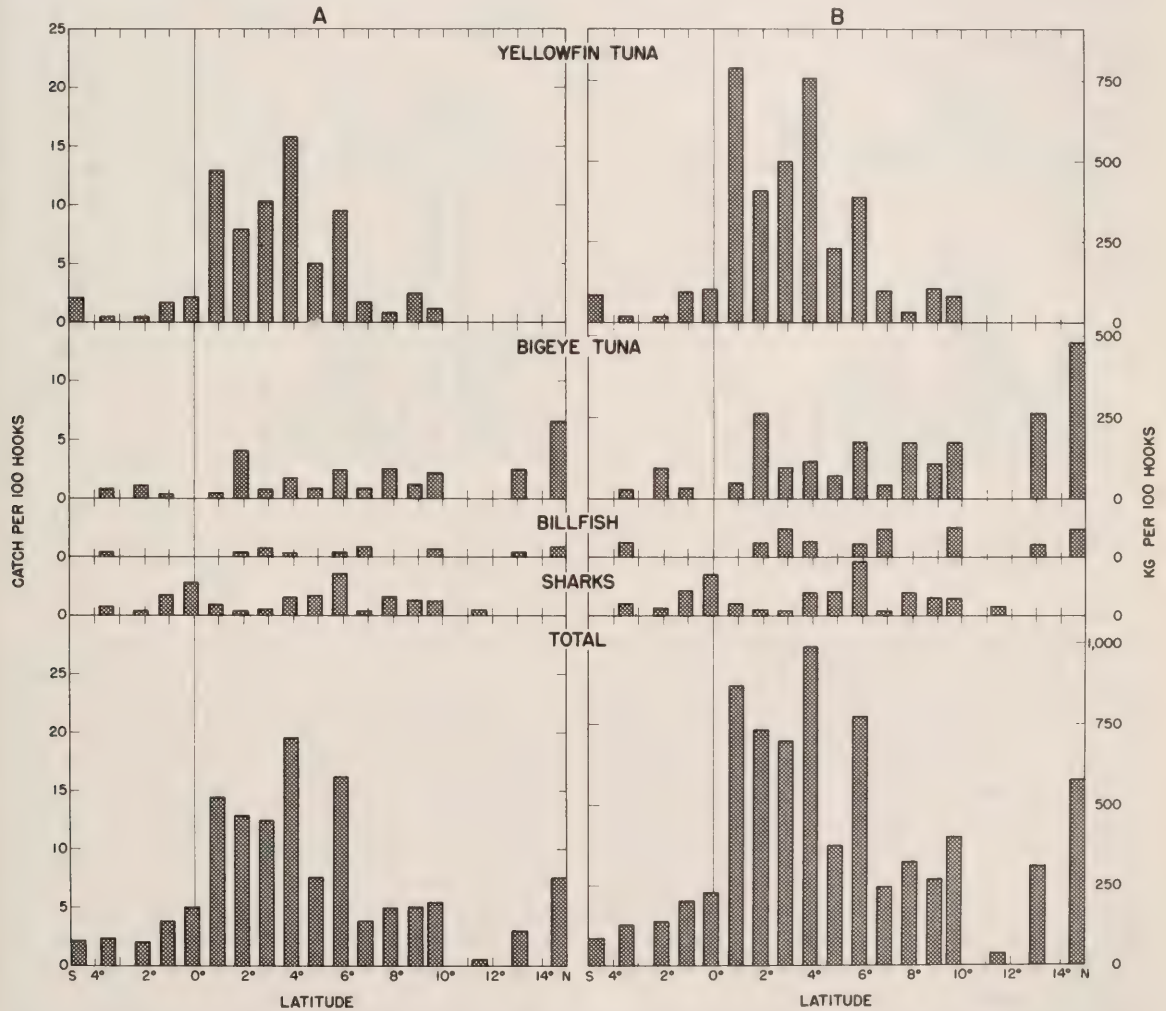
APPENDIX A

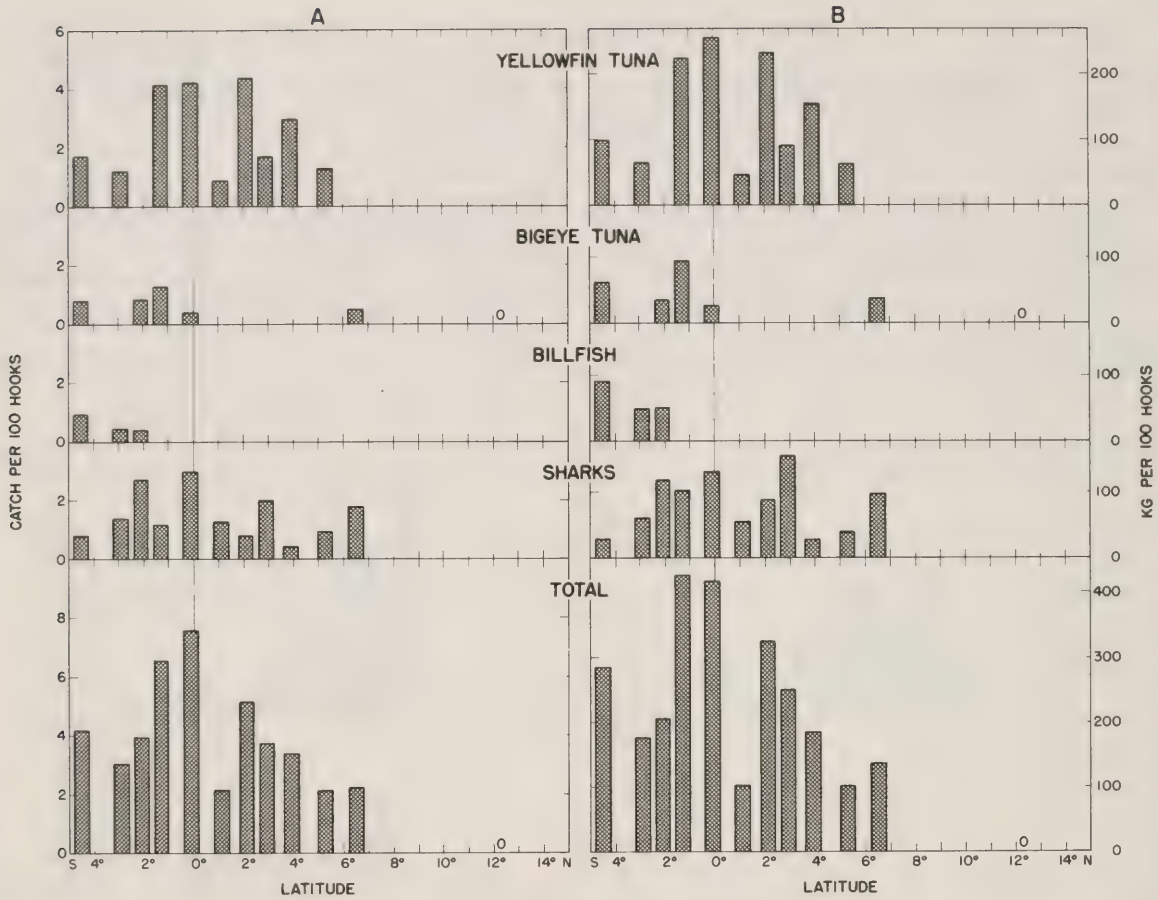
VALIDITY OF YELLOWFIN TUNA AS AN INDEX OF THE TUNA-SHARK TROPHIC LEVEL

Throughout this paper we have compared the distribution of tuna with the distribution of certain biological and physical properties of the environment. We have examined these environmental properties in relation to the number of yellowfin and other tuna captured per 100 hooks. This procedure could lead to misinterpretation, if the size of the individuals taken varies significantly or if the relative abundance of species within a trophic level changes with respect to time or space.

Ideally, we wish to ascertain the relative



APPENDIX FIGURE 1.—Latitudinal distribution of longline-caught fish on long 150°W during August-September 1951, a period of good fishing success. A. Number of fish per 100 hooks. B. Weight (in kilograms) per 100 hooks.



APPENDIX FIGURE 2.—Latitudinal distribution of longline-caught fish on long 150°W during January-February 1953, a period of poor fishing success. A. Number of fish per 100 hooks. B. Weight (in kilograms) per 100 hooks.

weight of fish life at a given trophic level and compare that weight with other properties of the biosphere, e.g., standing crop of zooplankton. Uniform sampling of a given trophic level, especially if it comprises several species, is difficult. In the longline, however, we have a tool that appears to sample a reasonably restricted trophic level. All of the principal species taken are definitely carnivorous, as shown by their attraction to fish baits, so this characteristic defines and restricts the "trophic level." In the present instance the trophic level is composed principally of tunas, sharks, and billfishes.

Additional information that aids in defining the trophic level stems from studies of the food habits of the fishes. King and Ikehara (1956) have shown that the yellowfin and bigeye tunas in the central Pacific essentially share a common diet of small to medium-sized invertebrates and fishes. Recent studies suggest that the same statement applies to the skipjack tuna and albacore. Most pelagic sharks taken on the longline in the central Pacific also seem to share the tuna forage (Strasburg, 1958). Large billfishes, however, appear to represent a somewhat higher trophic level. The smaller items in their diet approximately coincide with the large items in the diet of the tunas and sharks. Thus, there are good grounds for considering tunas and sharks as representatives of a restricted trophic

level, but the inclusion of billfishes is open to question.

On the subject of numbers of fish versus weight, Appendix Figures 1 and 2 depict the results of two section lines along long 150°W, one representing good and the other poor fishing. The members of each pair of panels give the same impressions. In the first series abundance is very high between lat 1° and 6°N and considerably lower to the north and south. In the second series the total abundance is much lower, but the catches definitely peak between lat 2°S and 4°N. The inclusion or omission of the billfishes, thought to represent a slightly higher trophic level than the tunas and sharks, has little effect on the major trends.

We may draw two important conclusions from the plots of number and weight. Because the trends are nearly the same, the average size of each of the component species must change little, if at all, with latitude. Even more important, it is apparent that latitudinal variations in catch are largely a function of variations in yellowfin tuna abundance, particularly between lat 5°S and 5°N, the general area in which this study has been focused. Because the yellowfin tuna is the most important species in this region, we lose little biologically and gain much in ease of understanding by restricting comparisons of the fish population and the environment to yellowfin tuna.

One flaw in these arguments for considering yellowfin tuna only is our failure to take into account the skipjack tuna, for it almost certainly belongs to the same trophic level as the yellowfin tuna. Although small yellowfin tuna are almost absent from longline catches in the oceanic areas under consideration, skipjack tuna are strongly represented. In fact the available evidence suggests they are abundant to the north of the concentration of yellowfin tuna (lat 5°-10°N). We can offer no satisfactory solution, for it is not yet possible to combine quantitatively measures of abundance of deep-swimming fishes with those of surface fishes. In our opinion, however, if it were possible to add skipjack tuna to the weight diagrams of Appendix Figure 2, there would be little change in the relative distribution of the tuna-shark trophic level near the equator.

BEHAVIOR OF BLUEFIN TUNA SCHOOLS IN THE EASTERN NORTH PACIFIC OCEAN AS INFERRED FROM FISHERMEN'S LOGBOOKS, 1960-67[1]

J. Michael Scott[2] and Glenn A. Flittner[3]

ABSTRACT

Fishermen's records of 8,059 purse-seine sets made on *Thunnus thynnus* (bluefin tuna) were examined for the period 1960-67. A total of 3,538 sets were identified as to school type. The majority of these sets were made within 90 miles of the beach off southern and Baja California from lat 23°N to 34°N. The region was divided into a northern and southern area on the basis of biological and oceanographic factors.

Significant differences were observed in the occurrence of the six most common school types between the northern and southern most areas of the fishery. The difference in occurrence of the jumping, boiling, and shining schools was related to the relative absence of red crabs (*Pleuroncodes planipes*) in the northern area and to differences in the foraging behavior of *T. thynnus* on baitfish and red crabs.

Differences in vulnerability to capture and catch per successful set were noted among the five most common daytime schools as well as with respect to time of day.

Purse-seine sets made with the assistance of airborne spotters had larger catches and a greater percentage success than did unassisted sets. In addition the percentage of a particular school type taken with aircraft assistance was inversely proportional to the visibility of the schools from the mast.

The existence of different school types in scombroid fishes has been noted by several authors. In 1931, Suzaki (as cited by Uda, 1933) recognized five types of skipjack tuna (*Katsuwonus pelamis*) schools in the western tropical Pacific. Kimura (1954) listed six types of skipjack tuna schools. To these Inoue (1959) added three additional types based on behavior and association of the tuna with animals and inanimate objects. Ogilvie (1949)[4] described 10 types of tuna schools commonly encountered in the eastern tropical Pacific. McNeely (1961) stated that the California tuna fishermen recognized several different school types for yellowfin (*Thunnus albacares*), skipjack, and bluefin tuna (*T. thynnus*). Scott (1969) described 16 different school types for the eastern Pacific tunas, listed fishermen's synonyms, and placed them into two major groups and five lesser categories on the basis of time of day, depth of occurrence, and association with other animals and floating objects.

Various attempts have been made to correlate the type of school with fishing success. Uda (1933) and Uda and Tukusi (1934) attempted to show an "index of biting" for the different school types as did Kimura (1954). Inoue (1959) correlated the percentage success of the Japanese purse seiner fleet with school types for yellowfin, skipjack, and bluefin tuna in the western tropical Pacific. Inoue's data indicated that possible differences in school size and vulnera-

[1] This work was initiated while both authors were employed in the Tuna Resources Laboratory of the Bureau of Commercial Fisheries (now the National Marine Fisheries Service, Southwest Fisheries Center) under the direction of Dr. Richard R. Whitney, then leader of the Tuna Behavior Program.

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[4] Ogilvie, H. 1949. Description of various types of tuna schools, of behavior, methods of fishing and production possibilities in relation to pole and line fishing encountered in Central America. Inter-American Tropical Tuna Commission, La Jolla, Calif. 5 p. (Manuscr.)

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FISHERY BULLETIN: VOL. 70, NO. 3, 1972.

bility to capture existed among the various school types as well as between the three species.

MATERIALS AND METHODS

In order to describe the schooling behavior of *T. thynnus* in the eastern North Pacific and to relate this behavior to percentage of successful sets and catch per successful purse-seine set, California fishermen's logbooks were analyzed for the period 1960-67. Abstracts of these logs were made available through the courtesy of the Inter-American Tropical Tuna Commission.

A purse-seine set is defined as that operation in which the net is laid out around a school of fish and the bottom of the net drawn together, capturing the fish, which are then transferred to the vessel (Orange, Schaefer, and Larmie, 1957). A complete description of the fishing operation is given by McNeely (1961). For the purposes of this paper the term "school" will apply to that quantity of fish captured in a successful set of the net. No assumptions as to the configuration of the school nor the orientation of the fish within the school will be made (see Williams, 1964; Breder, 1967).

Orange, Schaefer, and Larmie (1957) made several assumptions in analyzing single set data from fishermen's logbooks, and other workers have followed (Broadhead and Orange, 1960; Whitney, 1969). These assumptions are:

1. A set of the net is made on a single school of fish.
2. Either the entire school is captured or each set captures a constant fraction of the school upon which it is made.
3. Vessel masters can estimate accurately the tonnage from individual sets of the net.

In addition, it is assumed that the schooling behavior described in ship's logs indicated the school type evident when the fish were first observed.

The average size of all schools may actually be smaller than those cited by the fishermen because small schools of 2 tons or less may be passed over by the fishermen in the hope of capturing a larger school later in the day.

In regard to the second assumption, fishermen generally agree that it is extremely difficult to "cut" a tuna school with their nets; it appears to be an all-or-nothing situation. Typically a fisherman will catch ¼ ton or less when the school is missed. These fish usually are entrapped in net folds during the pursing operation and are unable to escape with the main body of the school being set upon. The constant fraction, therefore, approaches zero. That the second assumption does not hold in every case was recognized by the original proponents (Orange, Schaefer, and Larmie, 1957). We have assumed also that the fraction of fish retained in the net from a school escaping capture is the same for all school types, as well as for all times of day; these are factors which need additional study.

Fishermen identify schools to species with considerable skill, but the system of identification is difficult to describe. Their ability to judge tonnage, however, is very good after the fish are inside the net and in full view of the mastman. The airborne spotters are extremely good at estimating school size.

Bluefin net sets were defined to be: 1) all sets in which 90% or more of the total tonnage landed was *T. thynnus*, 2) all no-catch sets in which *T. thynnus* was clearly identified as the pursued species, and 3) all sets in which it could be determined from location, water temperature, date, time, and previous and later sets by the same or other boats operating nearby that it was *T. thynnus* being sought and/or captured. Using the above criteria, we determined that a minimum of 8,059 sets were made on *T. thynnus* and 65,478 tons landed by the eastern North Pacific high seas purse-seine fleet during the period 1960-67. Of these sets, 43.9% were identified in the logbooks as to school type.

All weight references in this paper are expressed in short ton units.

SCHOOLING BEHAVIOR

The terminology of school types used in this paper is that of Scott (1969) (Table 1). *T. thynnus* exhibited 13 different types of schooling

TABLE 1.—Terms used by southern California purse-seine tuna fishermen to describe various types of tuna schools and associations (from Scott, 1969).

School fish	Associated schools[1]
Surface schools[1]	Fish and mammals[1]
Breezer	Porpoise schools
Finner	Spotters
Jumper	Spinners
Boiler, foamer, smoker, or meatball	Spotters and spinners
	Whitebelly
	Whale schools
Subsurface schools[1]	
	Shark schools
Black spot, dark spot, brown spot, green spot, or black ball	Inanimate object association[1]
	Log school
Shiner	Bait boat
Night schools[1]	
Fireball, ardura, glow spot, white spot, or flare	
Popper	

[1] These terms are used for organization of the table and are not used by the fishermen.

behavior and 12 different combinations of these to the commercial fishermen. There were differences in frequency of occurrence, size of the schools, and vulnerability to capture between the schools (Table 2). Differences in the occurrence of the school types in the northern and southern areas of the fishery were also evident (Table 3).

In order to eliminate possible bias in analyzing school size and percentage success, all sets made with the assistance of airborne spotters have been separated. The effects of airborne spotters on catch data will be discussed later in this paper.

Of the 13 school types observed, only 6 were recorded often enough (50 or more times) to warrant attention.

GEOGRAPHICAL VARIATION

T. thynnus is taken along the coast of Baja California and southern California from lat 23°N to 34°N. Occasionally fish are taken north of this area, especially in warm water years, but they are few, and seiner operations are severely limited by prevailing weather and sea conditions. The greatest percentage of the bluefin catch is made within 90 miles of shore near shoals, banks, reefs, and islands.

We have divided the area of the fishery into two major areas: that area north of lat 28°59'N and the area south of and including that same latitude (Figure 1). There is some biological basis for this division, as Punta Eugenia marks the northernmost extension of the Panamic fauna (Steinbeck and Ricketts, 1941). In addition, oceanographic and meteorological conditions also differ considerably. South of Punta Eugenia, an annual visitation of warm tropical

TABLE 2.—Catch statistics for 13 different bluefin school types and 4 different categories of combined schooling behavior observed.
[All purse-seine sets recording schooling behavior are included.]

School type	Total sets	Successful sets		Total catch (short tons)	Average catch per successful set (short tons)
		Number	Percent		
Breezers	1,871	870	46.5	17,043	19.6
Boilers	221	141	63.8	1,286	9.1
Jumpers	639	414	64.8	2,192	5.3
Black spots	137	61	44.5	1,475	24.2
Shiners	111	67	60.4	776	11.6
Foamers	7	5	71.4	104	20.8
Fireballs	397	293	73.8	4,423	15.1
Finners	7	5	71.4	45	9.0
Log	1	0	0	0	0
Whales	15	6	40.0	91	15.2
Poppers	8	6	75.0	29	4.8
White spots	7	6	85.7	58	9.7
Meatballs	3	2	66.7	40	20.0
Combined schooling behavior recorded for the following					
Breezers	96	45	46.9	837	18.6
Boilers	4	3	75.0	68	22.7
Jumpers	10	8	80.0	68	8.5
Black spots	4	2	50.0	38	19.0
Total	3,538	1,934	54.7	28,573	14.8

TABLE 3.—Catch statistics for all non-aircraft assisted bluefin purse-seine sets recording schooling behavior.

School type	North of lat 28°59'N					South of lat 28°59'N					Northern and southern areas combined				
	Total sets	Successful sets		Catch per successful set (short tons)		Total sets	Successful sets		Catch per successful set (short tons)		Total sets	Successful sets		Catch per successful set (short tons)	
		Number	Percent	Median	Range		Number	Percent	Median	Range		Number	Percent	Median	Range
Breezers	475	206	43.4	10.5	0.3-100.0	1,037	492	47.5	14.0	0.5-145.0	1,512	698	46.1	12.0	0.3-145.0
Boilers	191	114	59.7	4.0	0.3- 73.0	13	7	53.9	25.0	4.0-106.0	204	121	59.3	4.0	0.3-106.0
Jumpers	572	363	63.5	2.0	0.2- 25.0	23	16	69.6	5.0	1.0- 44.0	595	379	63.7	2.0	0.2- 85.0
Black spots	17	5	29.4	9.0	4.0- 30.0	70	31	44.3	15.0	2.0-200.0	87	36	41.4	15.0	2.0-200.0
Shiners	39	29	74.4	8.0	1.0- 55.0	28	10	35.7	5.0	1.0- 15.0	67	39	58.2	7.0	1.0- 55.0
Fireballs	296	220	74.3	8.0	5.0-140.0	94	68	72.3	12.0	0.3- 65.0	390	288	73.9	9.0	0.3-140.0
Total	1,590	937	58.9			1,265	624	49.3			2,855	1,561	54.1		

FIGURE 1.—Area of the eastern north Pacific bluefin tuna fishery.

waters occurs (except for a narrow band of very cold, rich upwelled water near shore south to San Juanico). Red crabs (*Pleuroncodes planipes*) are abundant in this area. Winds and weather are generally favorable for purse-seine operations after mid-June, but in April and May strong northwest winds severely restrict fishing.

From Punta Eugenia to Point Conception, the southern California offshore area typically exhibits the warm Catalina Gyre in association with cold, upwelled water centered off Ensenada and to the north of Point Conception. Hydrographic conditions in this region favor good filter feeding for bait fishes, and winds and weather improve in late July through September. Seldom is this district too warm for bluefin.

The occurrence of the various school types in the northern and southern areas of the fishery is nonrandom (chi square 985.20, $P<0.001$). Perhaps the most striking difference is the almost complete lack of jumping and boiling schools in the southern area and the predominance of breezers in this same area (Table 3). These differences may reflect differences in the feeding behavior of *T. thynnus* on different prey

species. McHugh (1952) and Alverson (1963) found differences in the stomach contents of albacore, yellowfin, and skipjack tuna in different geographical areas. McHugh noted that red crabs were the dominant food item for albacore off the Baja California coast, while anchovies and other baitfish dominated in fish stomachs taken from southern California waters. Blunt (1958) noted that of 168 *T. thynnus* taken off California in 1957, 70% had been feeding on anchovies. Longhurst (1967) observed that during normal years the distribution of *P. planipes* reaches from the area of Cedros Island south, while the range extends farther north during warm water years. This distributional pattern includes the entire area from which jumpers and boilers were almost entirely absent. While baitfish, like anchovies, are found in the southern area, previously cited studies indicate that red crabs may be the preferred food item. Since *P. planipes* is a relatively weak swimmer and occurs in very dense concentrations off southern Baja California, a modified filter feeding such as Sette (1950) described for Atlantic mackerel (*Scomber scombrus*) might be employed by *T. thynnus* while feeding on red crabs. On the other hand, the vigorous pursuit by scombroids feeding on forage fish is well known (Magnuson, 1963; Whitney, 1969).

The lack of jumping and boiling schools in the southern area also may be due to differences in the behavior of *T. thynnus* feeding on *P. planipes* and baitfish and a preference for the former when available. Comparisons of stomach contents of *T. thynnus* from the three school types would provide the necessary test of this hypothesis, but such information is not available. However, analyses of stomach contents for yellowfin from an area in which *P. planipes* was the dominant food item and from a second area in which fish were the dominant item have been made (Alverson, 1963). Yellowfin sets, which were from these same two areas (but at different times in 1965) and which were identified as to school type, showed significant differences (chi square 17.27, $P<0.01$) in the occurrence of jumping, boiling, and breezing schools (Table 4). Greater numbers of jumping and boiling schools and reduced numbers of breezers occurred in the area in which fish were the dominant food item, whereas the opposite was true in the area where red crabs were the dominant item. This lends support to our hypothesis that these school types reflect behavioral differences in the feeding patterns of *T. thynnus* and other tunas on red crabs and baitfish.

TABLE 4.—Comparison of breezing, jumping, and boiling yellowfin schools from the Gulf of Guayaquil and Baja California.[1]

Area	Breezers		Boilers		Jumpers	
	Number	Percent	Number	Percent	Number	Percent
Baja California[2]	183	91.5	1	0.5	16	8.0
Gulf of Guayaquil[3]	121	77.1	11	7.0	25	15.9
Total	304		12		41	

[1] Schooling data are for 1965 (Inter-American Tropical Tuna Commission, unpublished data).
[2] Stomach contents: fish, 19.4%; red crabs, 78.1% (Alverson, 1963)
[3] Stomach contents: fish, 76.9%; red crabs, 0.0% (Alverson, 1963) red crabs do not occur in the Gulf of Guayaquil.

If, in fact, many of the breezing schools in the southern area of the fishery are feeding upon red crabs, one would expect to find a greater percentage of successful sets on breezing schools in this area when compared with breezing schools taken in the northern area of the fishery. However the observed differences are not significant (chi square 2.18, $P>0.20$). It might be that if feeding breezers and nonfeeding breezers were compared that differences in percentage success between the two areas would be found.

The greater number of fireball schools observed in the northern area of the fishery may reflect a difference in the distribution of bioluminescent organisms. However, persistent stratus overcast in the southern California offshore zone during summer results from upwelled water coursing southward from Point Conception. As a result of this stratus overcast, the fishermen's ability to see fireballs at night may be significantly enhanced by eliminating background illumination from the moon and stars. The phenomenon requires further study.

VULNERABILITY TO CAPTURE

There were significant differences in vulnerability to capture, as indicated by percentage of successful sets (Table 2), among the five most common daytime schools (chi square 62.32,

$P<0.001$). These differences in vulnerability are most likely related to behavioral differences which affect a school's ability to avoid capture. Other factors such as water clarity, depth of thermocline, and water temperature also may be important. Two of the three most vulnerable school types were jumpers and boilers, both of which can be described as violently active schools in which individual fish are often in pursuit of baitfish. Shiner schools were also highly vulnerable to capture, yielding success rates of over 58%. It may be that shiners are subsurface feeding schools in which the "shines" are reflections of the operculum or of the lateral or ventral surfaces of the fish as they twist and turn in pursuit of their prey (Scott, 1969).

Three factors may be responsible for the greater vulnerability of these "feeding" schools: 1) feeding schools lack the organization of nonfeeding schools; 2) individual fish in feeding schools are less aware of threatening stimuli than are nonfeeding fish, and 3) feeding schools are more likely to remain in a localized area. The first two factors would increase a school's vulnerability to capture by delaying the time at which the fish are aware of potential danger and also by increasing the elapsed time before the fish react as a unit to this danger. The third factor would make it easier for the fisherman to anticipate the position of the school when he sets upon it. Another factor which should be mentioned is that a greater percentage of actively feeding schools may be located in areas of upwelling where cold, nutrient-laden waters generally result in decreased visibility. The effect of water clarity on percentage success has been discussed by Hester and Taylor (1965).

Breezing schools are generally schools moving in a single direction, often making sudden changes in depth, which makes it difficult for fishermen to anticipate the position of the school relative to the boat before setting. Greater cohesiveness is apparent among breezing schools, and it appears that there is a greater awareness of potential danger than in feeding schools.

Blackspots are subsurface schools which are difficult to locate and to catch. The very nature of this school type suggests that a greater number of them might be expected to be found in areas with a deep thermocline and clear surface waters. Green (1967) has shown that schools encountered in areas with a deep thermocline are less vulnerable to capture than are schools found in areas with a shallow thermocline. In addition, the deeper a school is in the water column, the closer it is to one possible route of escape: the bottom of the net. All of these factors would contribute to the greater rate of escapement observed for black spots.

We have omitted from this section any consideration of fireball schools. The reasons for the greater vulnerability of nighttime schools (discussed in a later section) are equally applicable to fireballs.

CATCH PER SUCCESSFUL SET

There were significant differences in the mean size of the six most common schools (Figure 2). Black spots and breezers were the two largest school types. The three feeding school types, jumpers, boilers, and shiners, were the smallest. The disruption of schooling behavior during feeding activity (Magnuson, 1963; Whitney,

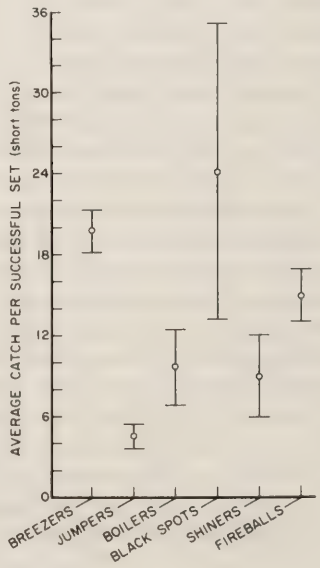

FIGURE 2.—Average catch (short tons) of each of the six most common bluefin tuna school types.

1969) may account, in part, for the reduced size of these schools. However, the observed disruptions have occurred within a relatively small area and were in response to an immediately available food source. It seems unlikely that the area involved would exceed that area normally encircled by a purse seine. We believe that the reduced size of the actively feeding daytime schools is the result of the relatively larger nighttime schools separating into smaller foraging schools with the rapid onset of higher light intensities at dawn.

Various mathematical treatments have shown the advantages of schooling to predator and prey alike (Brock and Riffenburgh, 1960; Olson, 1964). Olson contends that the swept path of an individual predator, and hence its chances of encountering a prey species, would be greatly increased if it traveled in a school rather than singly. In addition, we suggest that there is an optimum school size (number of individuals within the school) for feeding. Beyond this size, there may be increasing duplication of individual visual fields, making it more efficient for the fish to break down into a number of smaller schools in order to increase the area covered and thereby increase their chances of encountering and capturing prey. It may be also that individuals in schools beyond a certain size obtain less energy than those foraging in smaller schools. This school size would be dictated by a number of factors, such as visual acuity of the predator, type of prey, and prey density. A patchy distribution of a relatively fast moving schooling prey (e.g., anchovies) and a relatively uniform distribution of a slow moving prey (e.g., red crabs) within a localized area require different hunting and feeding strategies. Other factors may also be important (see Shaw, 1962; Breder, 1967).

TIME OF DAY

Fishermen recorded time of day for a total of 4,925 sets. Of these, 4,144 were made without aircraft assistance. The number of sets varied with time of day (Figure 3), as did the catch per successful set (Figure 4), percentage of successful sets (Figure 5), and occurrence of the various school types (Figure 6).

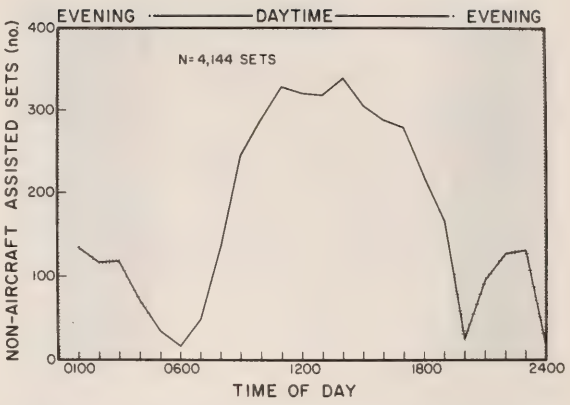

FIGURE 3.—Variation of the number of purse-seine sets on bluefin tuna in relation to time of day.

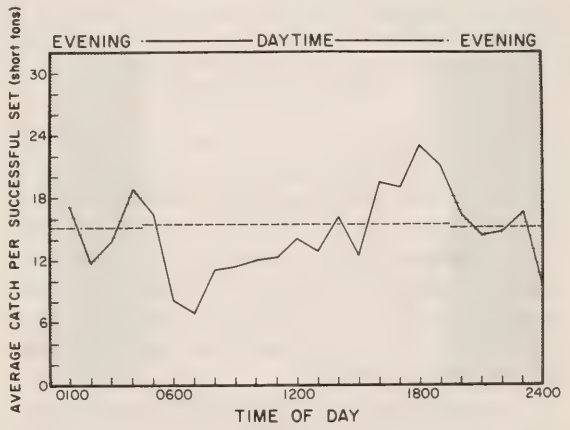

FIGURE 4.—Average catch per successful purse-seine set (short tons) on bluefin tuna in relation to time of day. (Not assisted by aircraft. Grand average catch for daylight and evening hours is indicated by the dashed lines.)

The percentage of successful sets on bluefin schools was significantly greater during the evening hours than it was during the day (chi square 126.56, $P<0.001$).

Whitney (1969) suggested that the greater vulnerability of tuna to capture at night was due to decreased visibility of the net and decreased activity of the fish. Recent laboratory work using *Engraulis mordax* has shown a diel rhythm

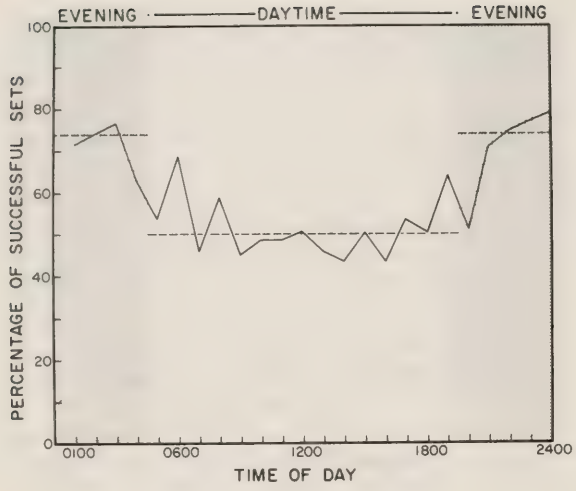

FIGURE 5.—Variation of percentage success of purse-seine sets on bluefin tuna in relation to time of day. (The grand average percentage success for daylight and evening hours is indicated by the dashed lines.)

in their direction of escape from a net cylinder (Scott, 1970). The tendency of *E. mordax* to use the bottom escape route during the day and to be random in their direction of escape at night would increase their vulnerability to capture at night by bottom-closing nets. If this same pattern is found in *T. thynnus* and other tunas, it would help to explain the observed differences in percentage success.

There were significant differences also in percentage success during the daylight hours (chi square 37.12, $P<0.01$). This is in contrast to the lack of significant variation in percentage success during the day reported by Whitney (1969).

The distribution in time of the five most common daytime school types is nonrandom (chi square 259.15, $P<0.001$). The three actively feeding schools were most common from 0700 to 1100 (Figure 6). During this period, these school types account for more than 42.2% of the identified school types.

The greater number of feeding schools in the early morning hours reflected in an increased percentage success during the early morning hours (0500-0800) when all school types are combined (Figure 5). The decrease in percent-

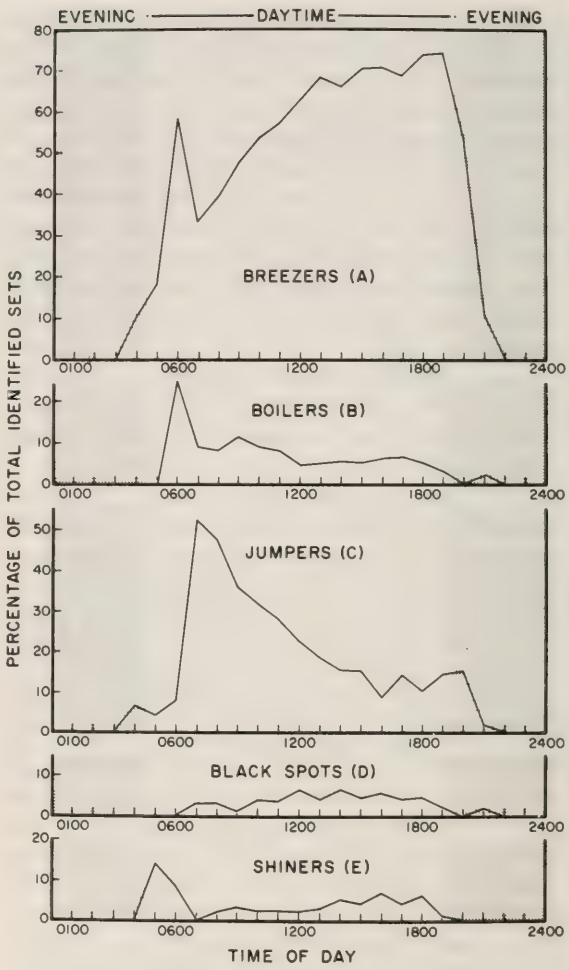

FIGURE 6.—Variation of occurrence of the five most common bluefin tuna school types in relation to time of day.

age success at 0700 is accounted for by a decrease in the percentage success of nonfeeding schools rather than a decrease in the number of feeding schools or a decrease in the vulnerability of feeding schools to capture. While the number of feeding schools increases until 1100, this is not reflected in an increase in the overall percentage success because of an accompanying increase in the number of nonfeeding schools (Figure 6). There appears to be a slight increase in the percentage of feeding schools during the late afternoon hours (1600-1900) (Figure 6B,C,D) which suggests that there may be two peaks in feeding

activity for *T. thynnus*, as has been shown for albacore (Iversen, 1962), bonito (Suyehiro, 1938), and yellowfin tuna (Uda, 1940; Waldron and King, 1963). However, the late afternoon increase in feeding activity is a minor one.

The percentage success does not vary significantly with respect to time of day in the four most common school types: breezers, jumpers, boilers, and fireballs (Figure 7). However, there is an increase in percentage success during the late afternoon hours for the three daytime schools, suggesting that the observed increase in percentage success during the late afternoon hours is due to the environmental factors cited by Whitney (1969). Additional data are needed for the late afternoon hours in order to further clarify this question.

The differences in school size between daytime (14.8 tons) and nighttime sets (14.4 tons) were not significant. However, there were differences noted in distribution of sets by 5-ton intervals (chi square 18.80, $P<0.05$) with fewer small schools (5 tons or less) being taken at night. The reduced percentage of small schools could be the result of a greater number of these schools being passed up by the fishermen at night, possibly because of reduced visibility to the mastman. We have no evidence to suggest a real decrease in the number of small schools during night hours as opposed to daytime.

There was a marked variation in average school size within the daylight hours; the size of schools steadily increased from 6.9 tons at 0700 to 22.5 tons at 1800 hours (Figure 5). This pattern is not apparent in the jumping and boiling schools, however (Figure 8).

The early morning decrease in school size initially may be a response to increased light and feeding activity as suggested by Whitney (1969); subsequently the relatively large nighttime schools break down into several smaller foraging schools and begin their search for food. The time elapsed between the reduction in school size and subsequent occurrence of large numbers of feeding schools might thus be the time required to encounter prey and begin to feed. We believe that the reduction in the number of feeding schools after 1100 hours reflects an increasing number of fish whose hunger is sated.

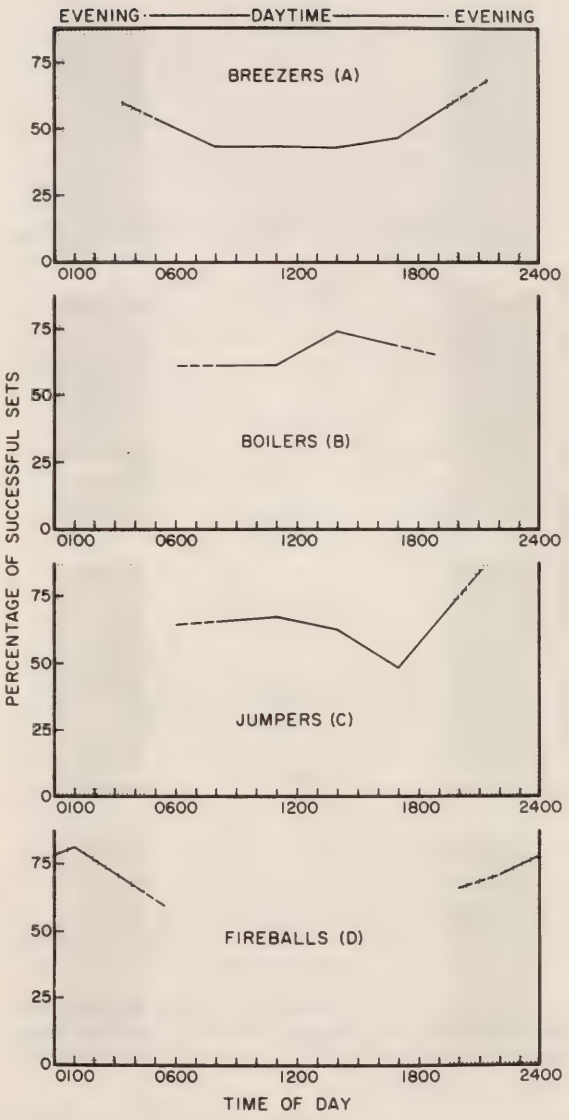

FIGURE 7.—Variations of percentage success on the four most common bluefin tuna school types in relation to time of day.

The gradual increase in school size during the daylight hours may be due to regrouping of the smaller schools through random encounters as suggested by Whitney (1969). The reduction in school size in the late afternoon cannot be accounted for by an increase in the number of

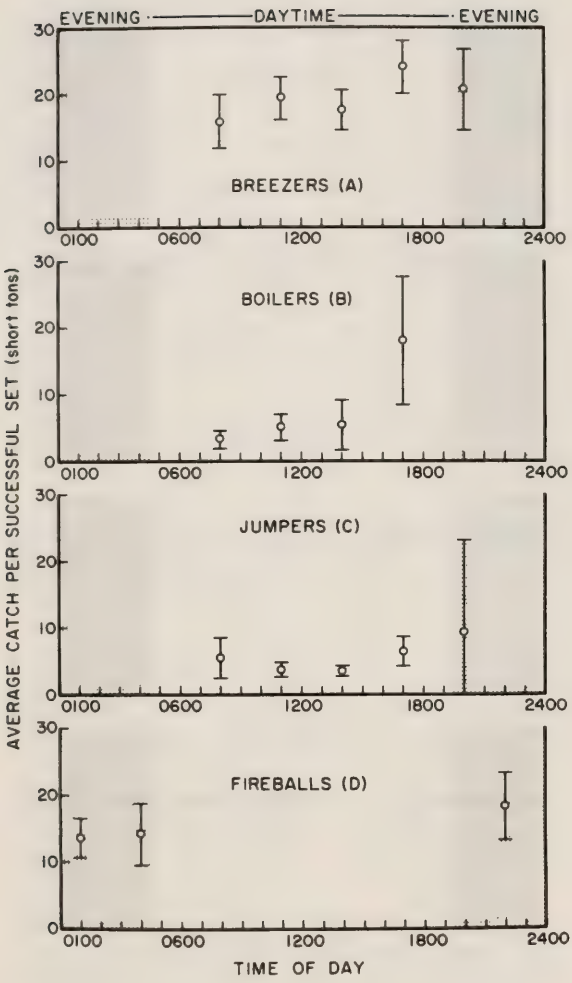

FIGURE 8.—Variation in the average catch per successful set on the four most common bluefin tuna school types in relation to time of day. (Catch in short tons grouped by 3-hr intervals.)

feeding schools and is most likely due to a reduction in available light (Whitney, 1969).

The lack of significant variation in either percentage success or catch per successful set within a single school type suggests that the observed variations in these two factors when all school types are considered together is due more to differences in the occurrence of the various school types within the daylight hours than it is to environmental factors such as daylight. However, the increased vulnerability of breezing and jumping schools during the late afternoon hours may be due to reduced light intensity during that period. Unfortunately it is the early morning and late afternoon hours for which we have the fewest data.

EFFECT OF AIRCRAFT ASSISTANCE

Aircraft assistance on bluefin tuna sets gave a significantly greater percentage of success than unassisted sets (chi square 8.69, $P<0.01$). The average catch in assisted sets also was consistently larger than in unassisted sets (Table 5). These differences have also been shown for yellowfin and skipjack tuna. The reasons for the greater size and vulnerability of schools set upon with aircraft assistance have been discussed elsewhere (Schaefer, 1962). In addition, however, the greater average size of assisted sets may be due to the disproportionately fewer small schools (jumpers and boilers) and a greater number of large schools (black spots and shiners) captured with aircraft assistance.

The two most visible schools, jumpers and boilers, have the smallest percentage of assisted sets (Table 6). The greater height of the air-

TABLE 5.—Effect of aircraft assistance on purse-seine sets for bluefin tuna, 1960-67.

Year	Percentage of sets assisted by aircraft	Percentage success		Catch per successful set (short tons)	
		Assisted	Unassisted	Assisted	Unassisted
1960	2.5	75.0	47.3	65.7	29.3
1961	14.5	79.0	63.8	17.7	12.6
1962	12.6	72.2	65.7	17.1	9.8
1963	20.4	45.8	41.2	20.5	21.2
1964	12.1	62.8	59.5	13.3	9.3
1965	20.2	43.4	48.0	19.3	14.7
1966	13.9	60.5	46.6	22.5	15.9
1967	11.5	51.5	43.1	23.6	19.5
Average	15.3	54.9	53.0	19.3	14.2

TABLE 6.—Comparison of effectiveness of aircraft assistance by school type for purse-seine sets on bluefin tuna, 1960-67.

School type	Number of sets	Aircraft assisted sets	
		Number	Percent
Boilers	221	17	7.7
Jumpers	639	44	6.9
Breezers	1,871	359	19.2
Shiners	111	44	39.6
Black spots	137	50	36.5
Totals	2,979	514	17.3

TABLE 7.—Comparison of average catch per successful set and percentage success for assisted and unassisted sets on the four most common daytime bluefin tuna school types.

School type	Average catch per successful set (short tons)		Percentage success	
	Assisted	Unassisted	Assisted	Unassisted
Jumpers	29.1	4.7	87.5	63.7
Breezers	21.3	19.8	47.9	46.2
Shiners	15.2	9.0	63.6	58.2
Black spots	23.0	25.0	50.0	41.4

craft and, therefore, the greater area and depth of visibility to an airborne spotter would increase the possibility of spotting the subsurface schools which otherwise might not be visible to observers aboard a vessel (Green, 1966).

However, there are differences in both catch per successful set and percentage success between assisted and unassisted sets in the same school type (Table 7). All of the schools show increased percentage success with aircraft assistance, and all but black spots exhibit larger school size with aircraft assistance. This indicates that the larger size and greater vulnerability of schools set on with aircraft assistance is the result not only of the unequal distribution of the various school types between assisted and unassisted sets but also due to the skill of the airborne spotter in locating larger schools, and by his ability to increase the ship's chances of capturing the school.

MULTIPLE SCHOOLING CHARACTERISTICS

Almost every possible combination of the 13 different school types occurred. However, schools recorded as showing two or more behavioral types made up a very small percentage of the total sets made. Whether this is indicative of the actual occurrence of these types or the propensity of the fishermen to record them and the log abstractor to copy them is unknown. The problem of multiple schooling types has been discussed elsewhere (Scott, 1969).

Bluefin were captured in sets with yellowfin, skipjack, and albacore. Bluefin were also observed schooling with whales (Table 1). In spite of large amounts of flotsam and jetsam occurring in the fishing area, only two reports of this school type were logged. No porpoise-associated schools were reported. This is probably due to the absence of porpoise in the areas in which bluefin are generally found. Further data are needed before meaningful conclusions can be drawn with respect to the occurrence or lack of porpoise-associated schools in the bluefin fishery.

DISCUSSION

Striking differences in catchability, size, and geographical distribution have been demonstrated for the various types of bluefin schools. Suggestions as to possible reasons for these differences are offered but in most instances additional behavioral information is needed. We hope that definitive field and laboratory behavioral studies will be made in order to further strengthen or disprove interpretations which we have drawn from the logbook data. Studies on other scombroids would also be valuable for comparative purposes. The possibility that there are two or more types of breezing schools should be studied in detail, and the percentage success of sets on breezing schools known to be feeding compared with nonfeeding schools should also be investigated.

ACKNOWLEDGMENTS

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and counsel. Dr. Richard R. Whitney originally suggested this study to us, and Dr. John R. Hunter gave valuable advice during the study. Roger E. Green assisted in constructing the original ADP format for data analysis. Dr. Richard Whitney, Dr. John R. Hunter, and Craig J. Orange reviewed the manuscript.

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NUTRIENT INVERSIONS IN THE SOUTHEASTERN TROPICAL PACIFIC OCEAN [1, 2]

WILLIAM H. THOMAS[3]

ABSTRACT

Nutrient inversions in the offshore southeastern tropical Pacific Ocean are described. At a typical station nutrients such as nitrate and phosphate are high at the surface, are at a minimum at about 100 m depth, and then increase at greater depths. Silicate follows this distribution to a lesser degree. These inversions occur from lat 8 to 15°S and are more pronounced in sections along long 126°W and 119°W than in sections farther east. The nutrient minimum is associated with water having a salinity maximum. It is suggested that such water may have acquired its characteristics in the mixed layer in areas to the south or southeast where the nutrients were depleted by phytoplankton, and has then sunk below high-nutrient and relatively fresh water carried westward from the Peru Current. However, the nutrients may also have been depleted in situ since the low-nutrient water contains a maximum amount of chlorophyll.

In water where nutrients are limiting phytoplankton growth, they are typically at minimum concentrations in the surface and mixed layer, increase at the thermocline, and reach a maximum below this depth. Such typical distributions are shown by Sverdrup, Johnson, and Fleming (1942) and by Riley and Skirrow (1965). The EASTROPAC data show such distributions in all parts of the nutrient-poor water of the northeastern tropical Pacific Ocean (Thomas, 1970, 1971, and unpublished data).

The purpose of this paper is to describe a different distribution occurring in the south tropical Pacific Ocean in which nutrient concentrations are typically high at the surface, are at a minimum at depths just above the permanent thermocline, and then increase at greater depths. In this paper this unusual distribution is called a "nutrient inversion."

METHODS

The EASTROPAC sampling program and vessel track charts are given in the Introduction to the EASTROPAC Atlas (Love, 1970). Nutrients (nitrate, nitrite, phosphate, and silicate) from Nansen bottle samples were analyzed with the Technicon® Autoanalyzer[4] using the methods of Armstrong, Stearns, and Strickland (1967) or manually, using methods outlined by Strickland and Parsons (1968). Vertical sections along given longitudes were plotted by computer (Love, 1970).

RESULTS

During February-March 1967, nutrient inversions were found at several stations near lat 10°S and along long 112°W, 119°W, and 126°W. A typical inversion is shown in Figure 1 for EASTROPAC Station 11.140; three nutrients—nitrate, phosphate, and silicate—show minima at

[1] Contribution from the Scripps Institution of Oceanography.

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[4] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

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about 60 to 140 m depth. The inversion is particularly pronounced for nitrate, where concentrations in the minimum reach nearly undetectable levels.

The inversions are also apparent in vertical sections. Section 11-NO_3-V2 from the EASTROPAC Atlas (Thomas, 1971) is shown in Figure 2. This section was taken along long 119°W in February 1967 and shows that the inversion extends from about lat 8° to 15°S.

Similar sections occupied in February-March 1967 showed the inversions along long 126°W (from lat 8° to 15°S) and along long 112°W (from lat 8° to 10°S). The nitrate data show inversions much more clearly than phosphate or silicate data. Inversions in nitrate concentration are barely detectable in sections to the east at these latitudes—along long 105°W, 98°W, or 92°W—because concentrations at similar depths are higher. The inversion phenomenon is most pronounced in the westerly sections of the EASTROPAC data.

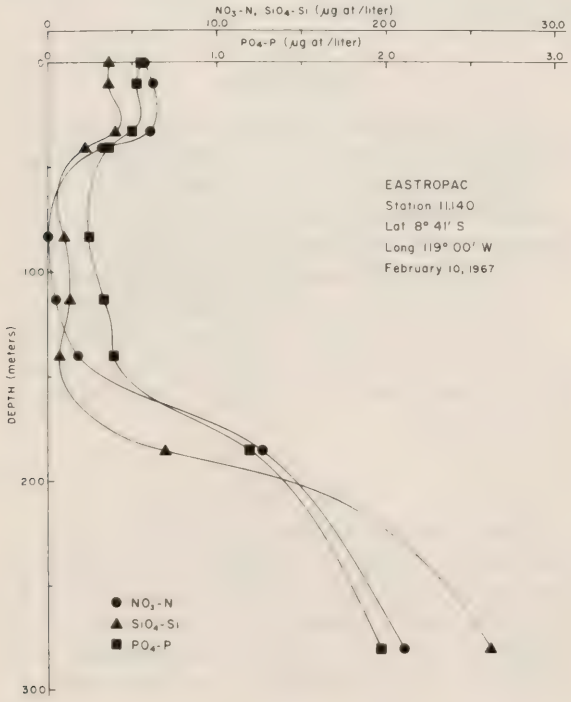

FIGURE 1.—Distribution of nitrate-N, silicate-Si, and phosphate-P concentrations with depth at EASTROPAC station 11.140, February 10, 1967.

The nitrate inversion was again detected in the southern summer of 1968 (February-March) during the third EASTROPAC survey (Thomas, unpublished Atlas data). At that time it was apparent along long 119°W (from lat 9° to 15°S), but not at more easterly longitudes. The long 126°W line was not sampled at this time.

It is not known whether inversions along these longitudes are permanent, nonseasonal features, since the second EASTROPAC survey during the southern winter (August-September 1967) and the EASTROPAC monitoring cruises (which took place between the multiship surveys) reached only lat 5°S. At this latitude inversions were not found.

DISCUSSION

Such nutrient inversions were not commented upon prior to EASTROPAC because this was the first expedition to measure a relatively complete suite of nutrients over a broad area of the eastern tropical Pacific Ocean. However, there are indications of such inversions in phosphate at many of the EQUAPAC stations taken in August-September 1956 during Cruise 35 of the RV *Hugh M. Smith* (Austin, 1957). The *Smith* traversed long 135°W, 143°W, 151°W, and 160°W from about lat 3°N to 19°S, and many of the stations taken from lat 5°S to 19°S show minimum phosphate values at about 100 to 160 m depth. The inversions probably would have been readily apparent if nitrate analyses had been made during *Smith* Cruise 35.

Such inversions are not found in stations taken from lat 7° to 15°S and long 162°W and 175°W in the nitrate, phosphate, or silicate data from cruise STYX in June-July 1968 (Reid, unpublished data). However, they are found to a slight extent in this same area when the nitrate data from a *Gascoyne* cruise in 1961 are examined (C.S.I.R.O., 1967).

This water having a minimum nutrient concentration has a high salinity. Figure 3 (from Tsuchiya, unpublished Atlas data) shows a salinity section along long 119°W in February 1967 from the EASTROPAC observations. The maximum in salinity clearly corresponds to the nutrient minimum shown in Figure 2.

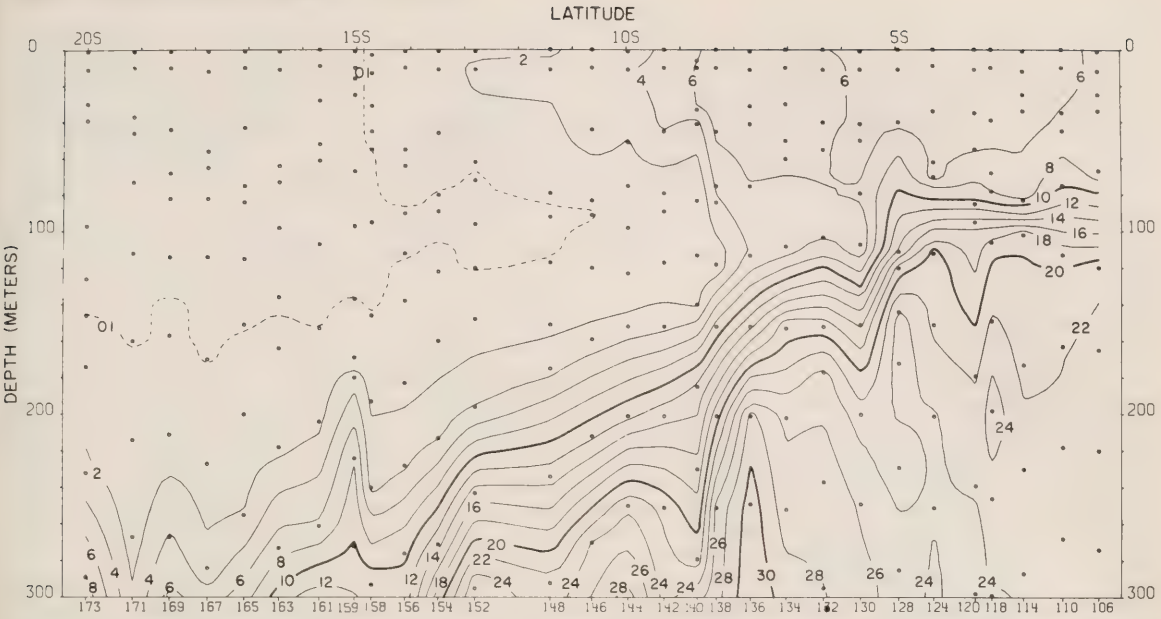

FIGURE 2.—Vertical distribution of nitrate-N (μg-at/liter) along long 119°W from lat 1°14'S to 20°00'S, February 7-14, 1967.

It is not easy to explain these distributions. There is a possibility that the subsurface water has been depleted of nutrients in situ since this water has a maximum chlorophyll concentration (Owen and Zeitzschel, 1971). On the other hand, one can envisage two water masses that impinge on each other. One of these, the low-salinity, high-nutrient, surface, and near-surface water, may have drifted to the west from the Peru Current via the South Equatorial Current. The horizontal maps of nutrients at 10 m (Thomas, 1971, and unpublished Atlas data) show that near-surface nutrients are high at these latitudes from Peru at least west to long 126°W, and Wyrtki (1966, Figures 1 and 2) indicates such westward surface currents. One can then envisage that the second water mass, containing high-salinity water that is depleted in nutrients, has its origin in the South Pacific Gyre and has sunk below the first water mass and drifted in from the southeast. Geostrophic flow of the maximum salinity water is predominantly from the east or southeast in the EASTROPAC area (Tsuchiya, unpublished Atlas observations) and similar flow from the east was shown by Tsuchiya (1968) in his Figure 6 for the 300 cl/t δ_t surface which has a depth of 50-100 m in this area. It should be mentioned that the data are very sparse in the area to the south and southeast of these inversions and their full explanation may await further data collection and analysis.

The nitrate data show the inversion more clearly than data for other nutrients, because nitrogen is more limiting to phytoplankton than phosphate or silicate in near-surface water to the south of these inversions (Thomas, 1969) and is possibly limiting in the water where the nutrients were depleted.

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Many persons aided in gathering these nutrient data during the EASTROPAC Expedition. Of these, Edward Renger and Don Seibert were of considerable help in analysing the data and preparing sections for drawing by the computer. I also thank Dr. Mizuki Tsuchiya and Joseph L. Reid for supplying data prior to its publication and for helpful discussions of the inversion phenomenon.

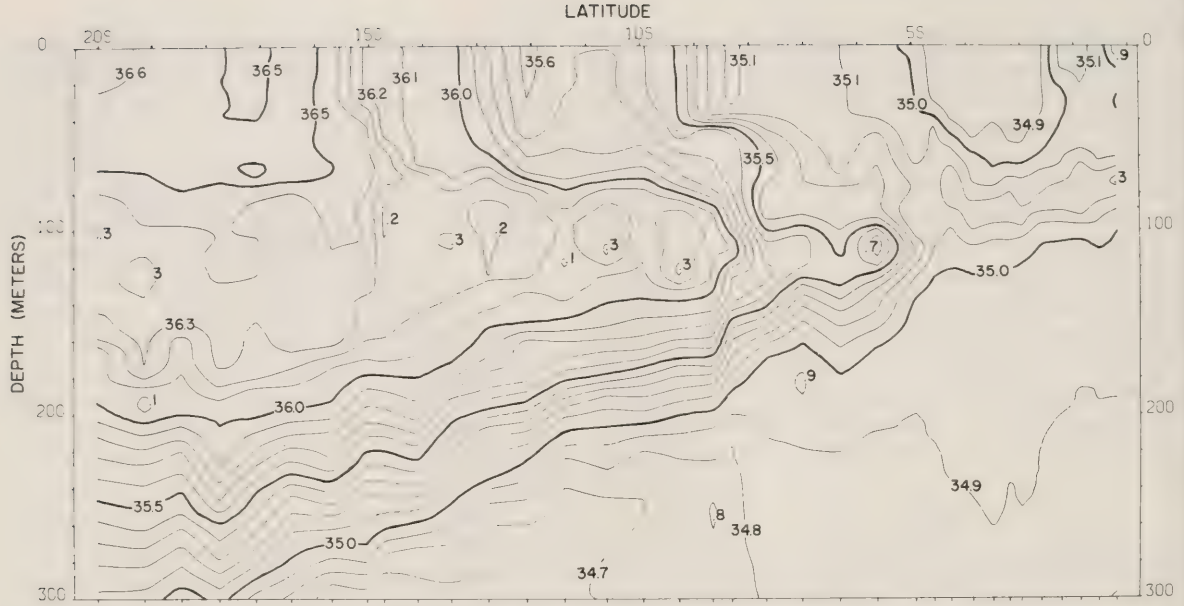

FIGURE 3.—Vertical distribution of salinity (‰) along long 119°W from lat 1°14′S to 20°00′S, February 7-14, 1967.

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GROWTH HORMONE- AND PROLACTIN-LIKE PROTEINS OF THE BLUE SHARK (*PRIONACE GLAUCA*)

U. J. Lewis[1], R. N. P. Singh[1], B. K. Seavey[1], R. Lasker[2], and Grace E. Pickford[3]

ABSTRACT

The two major disc-electrophoretic components, designated as "slow" and "fast," which are seen in fresh homogenates of the pars distalis of the blue shark (*Prionace glauca*) pituitary gland were isolated. Some alteration of the proteins occurred during the purification as evidenced by appearance of a slightly faster migrating band in each. The slow component and its altered form had a molecular weight of 22,000 daltons; the fast, and its modified form, 20,000 daltons. The two proteins were very similar chemically and immunologically, but definite differences were noted. Both gave a precipitin line with antiserum to mouse growth hormone, although quantitatively different, but neither reacted to antiserum to mouse prolactin. The peptide maps of the two proteins were identical except for three peptides. Both contained two moles of tryptophan and six half-cystine residues. These results indicate that the pars distalis of the blue shark contains two very similar proteins that resemble both growth hormone and prolactin of mammals.

There have been few reports that have dealt with the isolation of purified preparations of growth hormone and prolactin from pituitary glands of fish. This most probably stems from the fact that there is no convenient bioassay for these piscine hormones. Wilhelmi (1955) purified growth hormone from the hake; Donaldson, Yamazaki, and Clarke (1968) reported on prolactin of salmon; and Emmart and Bates (1968) described purification of prolactin of the pollack. As a means of circumventing bioassays, we thought that disc electrophoresis might prove successful. The method has been used by us to follow the purification of growth hormone and prolactin of the mouse (Cheever, Seavey, and Lewis, 1969), human (Lewis, Singh, and Seavey, 1971), and turtle (Singh, Seavey, and Lewis, 1972).[4] The approach appeared even more reasonable for the isolation of the shark hormones when we found that the electrophoretic pattern of the pars distalis extract contained only two major bands. This has been found to be the case for many species, and growth hormone usually has been identified as the slower migrating of the two bands (Nagy, Kurz, and Baranyai, 1969; Nicoll and Nichols, 1971; Nicoll and Licht, 1971). An exception to this has been found in the human (Friesen, Guyda, and Hardy, 1970; Lewis et al., 1971) where growth hormone is more acidic than prolactin and, therefore, migrates more rapidly during electrophoresis at an alkaline pH.

Making the assumption, then, that the two major bands seen in the electrophoretic pattern of the shark pituitary extract were growth hormone and prolactin, we devised a procedure for their isolation and used electrophoresis as a means of following the purification. The isolation procedure and some properties of the purified proteins are described in this communication.

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[4] Singh, R. N. P., B. K. Seavey, and U. J. Lewis. 1972. Purification and some properties of growth hormone and prolactin of the turtle. (Manuscr.)

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MATERIALS AND METHODS

DISC ELECTROPHORESIS

Our use of the method has been described (Lewis, Litteria, and Cheever, 1969). For routine analytical analyses the gel was made of 7.5% acrylamide and 0.25% N-N'-methylenebisacrylamide. For quantitation of the amount of protein in a stained band, ethylene diacrylate was substituted for the cross linking agent.

MOLECULAR WEIGHT

Molecular weights were estimated by using disc electrophoresis (Cheever and Lewis, 1969).

PEPTIDE MAPPING AND AMINO ACID ANALYSES

Our procedure for peptide mapping has been described (Seavey and Lewis, 1971). Total amino acid analyses were done on performic acid oxidized samples by means of automated analysis. Tryptophan was determined by the method of Beaven and Holiday (1952).

IMMUNODIFFUSION

Mouse growth hormone prepared by the method of Cheever et al. (1969) was used for immunization of monkeys; antiserum to mouse prolactin was produced in rabbits by using hormone prepared as described in the same publication. The antiserum to mouse growth hormone was not contaminated with antibodies to mouse serum proteins or mouse prolactin; the antiserum to mouse prolactin, likewise, did not give a precipitin line with serum proteins nor did it cross react with mouse growth hormone. Immunodiffusion was carried out by the method of Ouchterlony.

COLLECTION AND STORAGE OF GLANDS

The pars distalis was removed within 30 min after the animals were killed and immediately homogenized in water (5 ml/g wet tissue) at 5°C. The homogenate was stored at —20°C until it could be fractionated. This procedure was used to minimize alteration of the proteins, as judged by electrophoretic analysis. More rapid changes occurred when the glands were stored intact.

ISOLATION PROCEDURE

All processes were carried out at 5°C. The pars distalis (7.6 g wet weight) from 87 blue sharks were homogenized in 38 ml water. The pH of the homogenate was adjusted to 10 with dilute NaOH and made 10^{-3} M in diisopropylphosphofluoridate. After 4 hr of stirring the homogenate was centrifuged at 20,000 $\times$ g for 40 min. The supernatant fluid was decanted, its pH lowered to 8 with dilute HCl and set aside. The insoluble residue was suspended in 0.05 M Na_2CO_3-$NaHCO_3$ buffer, pH 10 (2.5 ml/g original tissue) and stirred for 16 hr. After centrifugation, the supernatant fluid was pooled with the first extract and the pH of the mixture adjusted to 8. The insoluble tissue was discarded when electrophoresis showed that all the desired components had been extracted.

The crude extract was concentrated to about 15 ml on a Diaflo UM-10 membrane[5] (Amicon, Lexington, Mass.) and placed on a column of Sephadex G-150, 5 $\times$ 90 cm and developed with 0.01 M NH_4HCO_3. Every fifth tube was analyzed by disc electrophoresis (100 μliter aliquots) and the tubes that contained the two proteins that were assumed to be growth hormone and prolactin were combined and concentrated to about 10 ml on a UM-10 Diaflo membrane. Figure 1 shows the elution pattern of the Sephadex column; the stippled area contained the desired components, S and F.

The concentrated solution from the Sephadex chromatography was applied to a column of DEAE-cellulose (Whatman 32) with dimensions of 0.9 $\times$ 10 cm and which had been equilibrated with 0.01 M NH_4HCO_3. The flow rate was 38 ml/hr. Once the sample had been applied, the column was washed with 25 ml of 0.01 M NH_4HCO_3. No appreciable amount of protein

[5] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

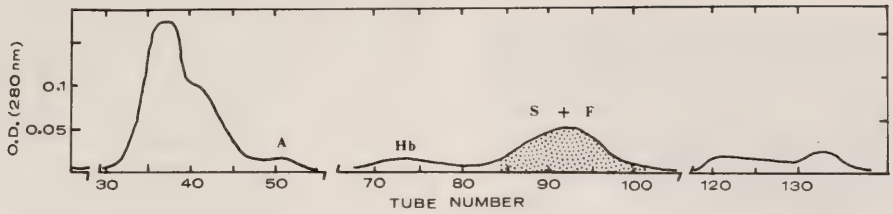

FIGURE 1.—Elution pattern obtained by chromatography of an alkaline extract of the pars distalis on Sephadex G-150. Each tube had a volume of 14 ml. The slow and fast electrophoretic components (S and F) were found in the stippled area. A = albumin; Hb = hemoglobin.

was eluted by the process. A gradient was next begun and was made by mixing equal portions (100 ml each) of 0.01 M and 0.1 M NH_4HCO_3. This eluted a major peak. A second gradient of equal volumes (150 ml each) of 0.1 M and 0.2 M NH_4HCO_3 was begun immediately. This gradient eluted a second peak. The results obtained with the DEAE-cellulose chromatography are shown in Figure 2.

The two major peaks eluted during chromatography on DEAE-cellulose were lyophilized. The yield of component F was 43 mg; that of component S, 22 mg.

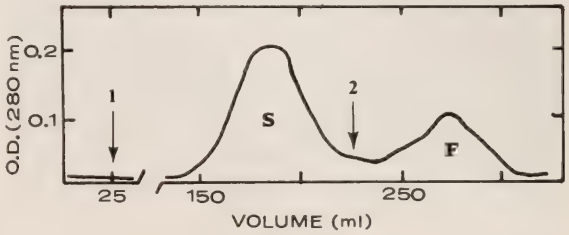

FIGURE 2.—Elution pattern obtained by chromatography of the S + F fraction of Figure 1 on DEAE-cellulose. The first gradient was begun at 1 and a second at 2. The S and F components were resolved as indicated in the drawing.

RESULTS

ELECTROPHORETIC ANALYSES

Pituitary Extracts

The water homogenate of the pars distalis showed two principal electrophoretic components when analyzed within 30 min after the sharks were taken from the sea. An alkaline extract of the glands, made about a week later, gave an almost identical pattern except that a definite band could be seen just ahead of each of the major components S and F. This is shown in Figure 3. The S and F components were assumed to be growth hormone and prolactin, respectively, and were the components for which we devised an isolation procedure. The bands designated as A, B, and C were minor components seen in both the water homogenate and the alkaline extract. A fast component also migrated near the buffer front.

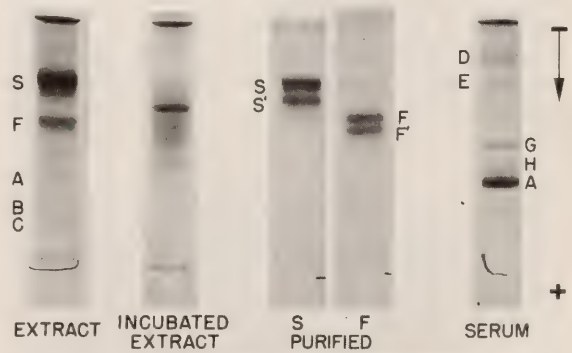

FIGURE 3.—Electrophoretic patterns (pH 9.5) of various shark materials. The pattern for the incubated sample was obtained after heating the alkaline extract at 37°C for 2 hr. S and F are the slow and fast components; S′ and F′ are the bands that formed during isolation of the proteins. Components A through E are discussed in the text. A thread marks the original buffer front (bromphenol blue) in two of the gels.

The conversion of the S and F bands to more rapidly migrating components became more pronounced as the fractionation of the extract progressed. As seen in Figure 3, by the time the proteins were isolated, each was a definite doublet. The new components are designated as S′ and F′. The same type of alteration of the S and F proteins occurred even during storage of intact glands at —20°C. After one month, the S′ and F′ were of about equal intensity to that of the original S and F bands. The alteration was barely noticeable however in a water homogenate of glands stored for the same length of time at —20°C. We determined also how incubation at 37°C affected the conversion of components S and F. After 2 hr at that temperature, S and F had virtually disappeared and a new band intermediate in mobility between S and F was present. This is shown in Figure 3. All bands disappeared if the extract was left at 37°C for 6 hr.

Serum

To determine whether either S or F might be serum components we analyzed a sample of shark serum (Figure 3). There was a faint band (E) in the region of S but none for F in gels of 7.5% acrylamide. At 10% and 12% acrylamide band E was more retarded than S, however. Component A of the pituitary extract lined up with the major component of serum in four concentrations of acrylamide.

PURIFICATION

The elution pattern obtained from chromatography of the alkaline extract on Sephadex G-150 is shown in Figure 1. As described in the experimental section above, the S and F components were located by disc electrophoresis and both were found in the same elution peak (stippled area). The peak of high molecular weight material at the beginning of the elution pattern gave an abnormally high optical density reading because of opalescence. The peak designated as A had the same electrophoretic properties of band A of Figure 3 and, as indicated above, was presumed to be albumin. The peak eluted just before S and F was labeled Hb (hemoglobin) because of its red color. Electrophoretically the material gave two very diffuse bands.

Figure 2 shows the elution pattern obtained by chromatography of Sephadex peak S + F on DEAE-cellulose. No protein was eluted with 0.01 M NH_4HCO_3. The first major peak, found to be F by electrophoretic analysis, was eluted by gradient 1 (0.01 M to 0.1 M NH_4HCO_3). A second gradient (0.1 M to 0.2 M NH_4HCO_3) eluted a second peak which was found to be component F by electrophoresis. The shoulder on the leading edge of peak F was probably a result of a small, rapid increase in ionic strength when the second gradient began.

The material of peaks S and F were lyophilized. The yield of S was 43 mg and 23 mg for F. Figure 3 shows the electrophoretic pattern of each of these samples. That each was a doublet was a result of alteration that took place during isolation. The conversion became progressively more pronounced during the purification.

MOLECULAR WEIGHTS

The molecular weights of components S and F as seen in electrophoretic patterns of the alkaline extract were S = 22,000 and F = 20,000. Identical values were obtained when the purified S and F fractions were analyzed. Likewise S′ and F′ had molecular weights indistinguishable from the corresponding S or F form although the molecular weight determination is accurate only to ± 2,000. The log R_m vs. gel concentration curves for these components are shown in Figure 4. Of significance was the fact that there was a greater charge difference between S and S′ than between F and F′. This is additional evidence that S and F are different substances. The slopes of the curves of Figure 4 were converted to molecular weight values by reference to a standard curve constructed from proteins of known molecular weight (Cheever and Lewis, 1969).

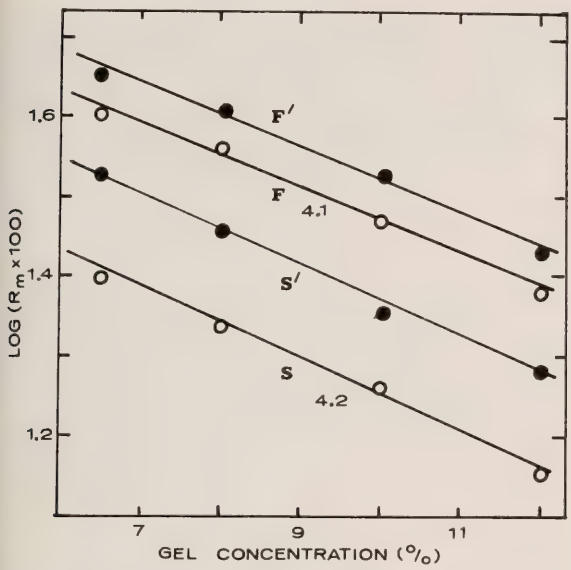

FIGURE 4.—A Ferguson plot of the relative mobility (R_m) of the S and F components and their altered forms (S′ and F′) versus the concentration of acrylamide used for the gel-electrophoresis.

The molecular weights of the other electrophoretic components seen in Figure 3 were A = 68,000; B = 65,000; C = 60,000; D = 47,000; E = 71,000; G = 64,000; H = 72,000.

IMMUNODIFFUSION

The purified preparations of S and F, which also contained S′ and F′, respectively, produced a precipitin line when tested against antiserum to mouse growth hormone (Figure 5). When tested at the same concentration, S gave a more pronounced line than did F. Neither preparation gave a precipitin line with antiserum to mouse prolactin.

AMINO ACID COMPOSITION

Table 1 gives the amino acid analyses of components S and F. The composition of the two proteins was quite similar but there were definite differences and component S had a greater total number of amino acids. Both contained six half-cystines and two tryptophans.

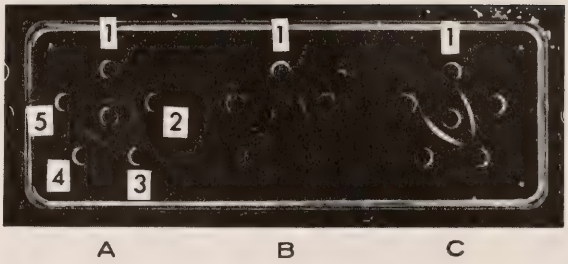

FIGURE 5.—Immunodiffusion plate for the S and F proteins. Antiserum to mouse growth hormone (10 μliter) was in the center well of A and B; antiserum to mouse prolactin was in the center well of C. The outer wells of A contained: **1**, 10 μg component S; **2** and **5**, 5 μg mouse growth hormone; 3, 5 μg component S; **5**, 2 μg component F. The outer wells of C contained: **1**, 10 μg component S; **2**, 5 μg mouse prolactin; 3, 10 μg component F; **4**, 5 μg mouse prolactin. The picture was taken after 24 hr at room temperature.

TABLE 1.—Amino acid composition of performic acid oxidized components S and F.

Amino acid	Component S residues[1]	Component F residues[1]
Cysteic acid	6.0	6.0
Aspartid acid	22.6	21.7
Methionine sulfone	4.8	4.0
Threonine	10.3	8.0
Serine	19.7	13.1
Glutamic acid	31.2	31.5
Proline	10.6	7.4
Glycine	10.2	8.4
Alanine	15.7	10.3
Valine	9.0	5.6
Isoleucine	6.3	6.9
Leucine	25.8	20.6
Tyrosine	6.9	3.8
Phenylalanine	10.1	7.2
Histidine	6.5	4.7
Lysine	17.5	15.0
Arginine	14.0	7.5
Tryptophan[2]	2.1	2.1

[1] Based on 22,000 daltons for S and 20,000 for F.
[2] Spectrophotometric (Beaven and Holiday, 1952).

PEPTIDE MAPS

Figure 6 is a drawing of the peptide map obtained with component S. The F component gave an almost identical map but was different in that peptides labeled S were not seen and another peptide labeled F was noted.

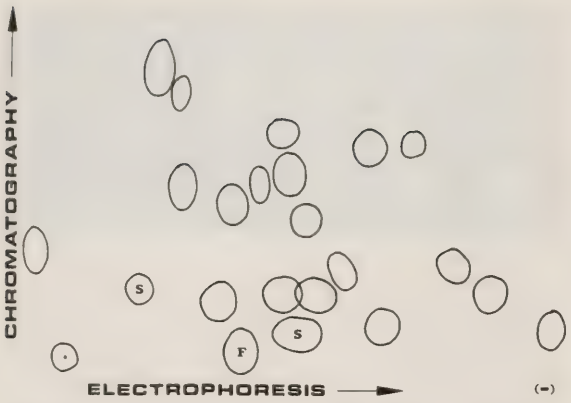

FIGURE 6.—Peptide map of a tryptic digest of component S. Chromatography was done with n-butanol-acetic-acid-water (4:1:5); electrophoresis was at pH 3.6 in a pyridine-acetic acid-water buffer (1:10:289). The peptide map of component F was identical except that peptides designated S were not seen and the peptide F was present.

DISCUSSION

From the immunodiffusion data we know that the S and F proteins are related to mammalian growth hormone. Their molecular weights also were near the values found for mammalian growth hormone and prolactin. One other observation which will be reported in detail later (Seavey et al., 1972)[6] was that the amino acid compositions of the tryptic peptides of the peptide maps closely resembled those of bovine growth hormone (Seavey et al., 1971). But because there were six half-cystine residues in both S and F and because each contained two residues of tryptophan, these two shark proteins are more like mammalian prolactins than the growth hormones which have only four half-cystines and one residue of tryptophan. Therefore, the proteins are not only very similar to each other, but are immunologically related to growth hormone and have structural resemblances to both growth hormone and prolactin. These results support the view that growth hormone and prolactin may have developed from a common ancestral protein. In the blue shark they appear as separate but yet quite similar substances with similarities to both growth hormone and prolactin. It will be interesting to see if there are two such proteins in the pituitary gland of cyclostomes.

If not already clear we would like to stress the point that no biological activities have been determined for the S and F components. Our assignment of growth hormone-like and prolactin-like properties are based on immunological and structural data alone. How these two components are related to the biological activities that have been reported for the shark pituitary gland is not known. Extensive biological studies are now needed to characterize these proteins. Also, more study will be given to the altered forms of the substances, and in particular the modification that was produced by incubation at 37°C. This type of study will be given to the altered forms of the hormones because of the rapid alterations that occurred even in the intact pituitary of the shark. We have observed that the prolactin activity of human growth hormone is increased when a hexapeptide is removed from the hormone by an enzyme present in pituitary extracts (Lewis et al., 1971). Biological activity of the shark hormones may also be affected by such changes. The nature of the alteration that occurs in the shark proteins is not known, but from our experiences with mammalian hormones we suspect that it is a result of deamidation, enzymic action, or a combination of both. The ease with which the shark's S and F components are converted to more acidic forms, however, strongly suggests deamidation, and the unusually large number of glutamic acid residues may actually be glutamines which rapidly lose ammonia.

ACKNOWLEDGMENTS

Much of this work was made possible by a grant from the National Institutes of Health (AM-09537). We also gratefully acknowledge the support given the project by the National Science Foundation in making the facilities of the RV *Alpha Helix* available for a 5-day cruise to study the pituitary of the blue shark. We are indebted to Dr. Y. N. Sinha of the Division

[6] Seavey, B. K., R. N. P. Sigh, U. J. Lewis, and R. Lasker. 1972. Tentative structure for a growth hormone-like, prolactin-like protein of the shark.

of Endocrinology, Scripps Clinic and Research Foundation, for the antisera used in these studies, and to Ronald Dotson and John LaGrange of the National Marine Fisheries Service for their assistance in catching the sharks.

ADDENDUM

The S component of the shark pituitary gland was tested for its ability to produce growth in hypophysectomized *Fundulus heteroclitus*. The results are shown in Figure 7. The preparation was found to be as potent as a previously assayed sample of hake growth hormone (Wilhelmi, 1955).

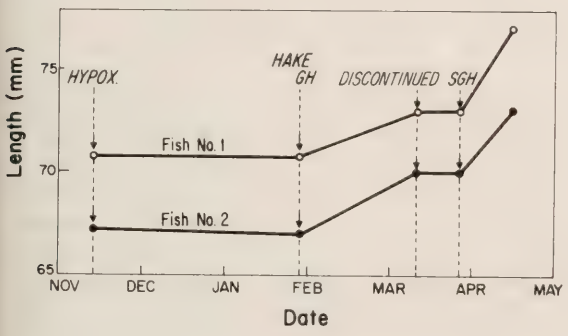

FIGURE 7.—Growth of two hypophysectomized male *Fundulus heteroclitus* after administration of growth hormone. Eleven weeks after hypophysectomy (HYPOX), injections of hake growth hormone (HAKE GH) (Wilhelmi, 1955) were begun and continued for five weeks. The injections were discontinued for two weeks and then resumed with shark growth hormone (SGH) for a period of four weeks. The S component of the shark pituitary gland was used. Both the hake and shark growth hormones were injected three times weekly at a dosage of 20 μg of hormone per gram (wet weight) of fish.

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DEVELOPMENT AND GEOGRAPHIC DISTRIBUTION OF THE ROCKFISH, *SEBASTES MACDONALDI* (EIGENMANN AND BEESON, 1893), FAMILY SCORPAENIDAE, OFF SOUTHERN CALIFORNIA AND BAJA CALIFORNIA

H. Geoffrey Moser[1]

ABSTRACT

The larval and juvenile stages of the scorpaenid fish, *Sebastes macdonaldi*, are described and illustrated. The sequence of ossification of bones and cranial spines in larvae is described in detail. *S. macdonaldi* appears to have the most southerly distribution of any species of *Sebastes* in the eastern north Pacific. The geographic distribution and seasonal abundance of *S. macdonaldi* larvae are discussed and compared with published information on the adults.

The genus *Sebastes* is represented by 65 species in the eastern north Pacific (Chen, 1971). Although all members of the genus are ovoviviparous and have a planktonic larval stage, they exhibit a remarkable diversity in morphology, color, and mode of existence. They rank first in total numbers of fish landed annually by the California sport fishing fleet (Young, 1969) and are a major commercial resource (Heimann and Frey, 1968). Despite their obvious importance, information on the complete life histories of all but a few species is fragmentary or nonexistent. At present a complete life history series (embryonic, larval, juvenile, and adult stages) has been described for only a single eastern Pacific species, *S. paucispinis* (Moser, 1967); however, young-stage larvae attained from pregnant females have been illustrated for four species from central California (Morris, 1956), for nine species from the Pacific northwest (DeLacy, Hitz, and Dryfoos, 1964), and for 14 additional rockfishes from southern California and Baja California (Moser, 1967). Recently, Waldron (1968) has described the early larvae of *S. pinniger*.

Ahlstrom (1961, 1965, 1969) has shown that rockfish larvae are the third or fourth most abundant kind of larvae collected annually in the plankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). Early juvenile rockfish, like the larvae, are pelagic but evade plankton nets easily and must be collected by other means. For example, some species are attracted to bright lights at night and can be dipnetted at the surface. Also, some species associate with floating objects (Hitz, 1961) and with drifting kelp (Mitchell and Hunter, 1970) and may be collected when these are brought aboard ship. Finally, pelagic juveniles occasionally appear in midwater trawl samples (Berry and Perkins, 1966; Lavenberg and Fitch, 1966). Demersal juveniles are common constituents of otter trawl catches in coastal waters.

Larvae of *S. macdonaldi* have such a distinctive melanophore pattern that a developmental series was established before it could be identified to species. The extreme southerly distribution of these larvae in the CalCOFI pattern provided a clue to their identity, since adults of *S. macdonaldi* have been collected farther south along Baja California than any other species of *Sebastes* (Chen, 1971). A comparison of intraovarian larvae from pregnant *S. macdonaldi* with the smallest individuals from plankton collections provided definitive evidence of the identity of the larval series. Juvenile stages critical

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to the completion of the developmental series were obtained principally from midwater and bottom trawls. These developmental stages are described herein, with special emphasis on the developmental osteology of the larvae. Also, the geographic distribution of the larvae in the CalCOFI area is presented and compared with the known distributions of juveniles and adults.

METHODS

Larvae of *S. macdonaldi* from 4 years (1953, 1960, 1965, 1966) of CalCOFI survey cruises were identified and counted. From these and selected other specimens, two developmental series that encompassed the entire larval period were established. Larvae of the first series were measured with the ocular micrometer of a stereoscopic microscope to produce a table of morphometrics (Table 1) for comparison of body proportions of *S. macdonaldi* larvae with those of *S. paucispinis* and other species. This series also provided a framework for the descriptions of larval morphology and melanophore pattern. Larvae of the second series, cleared with a graded series of KOH-glycerin solutions and stained with Alizarin Red-S, were used to determine the sequence of ossification of bones and fin rays and to prepare a table of meristic characters (Table 2).

TABLE 1.—Measurements (mm) of larvae and pelagic juveniles of *Sebastes macdonaldi*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Snout-anus distance	Head length	Snout length	Upper jaw length	Eye diameter	Interorbital distance	Body depth	Pectoral fin length	Pelvic fin length	Snout to origin of anal fin	Snout to origin of pelvic fin
SIO 65-230	4.5	1.8	1.1	0.38	--	0.37	0.60	0.90	0.27	--	--	--
CalCOFI 6602-117.40	4.7	1.8	1.2	0.30	--	0.45	0.53	1.0	0.40	--	--	--
CalCOFI 6604-123.36	5.0	1.8	1.2	0.30	--	0.46	0.60	1.0	0.33	--	--	--
CalCOFI 6604-117.30	5.2	2.1	1.4	0.48	0.72	0.51	0.68	1.2	0.36	--	--	--
CalCOFI 6604-113.55	5.7	2.4	1.6	0.47	0.67	0.57	0.63	1.3	0.52	--	--	--
CalCOFI 6604-113.55	5.9	2.6	1.8	0.48	0.76	0.55	0.60	1.5	0.45	--	--	--
CalCOFI 6604-107.31	6.3	2.8	1.8	0.56	0.76	0.57	0.87	1.6	0.60	0.05	--	1.9
CalCOFI 6604-93.28	6.7	2.9	1.9	0.56	--	0.63	0.86	1.7	0.61	0.04	--	2.1
CalCOFI 6604-127.40	6.8	3.1	1.9	0.55	0.95	0.70	0.95	1.8	0.62	0.15	--	2.2
CalCOFI 6501-117.45	7.0	3.3	2.1	0.75	1.1	0.70	1.1	1.9	0.60	0.12	--	2.3
CalCOFI 5304-117.45	7.6	3.5	2.2	0.79	1.1	0.73	1.1	2.0	0.68	0.20	--	2.3
CalCOFI 6602-110.40	7.7	3.8	2.7	0.82	1.2	0.84	1.2	2.3	0.90	0.33	4.2	2.5
CalCOFI 6605-117.35	7.9	3.8	2.7	0.82	1.3	0.90	1.2	2.5	0.93	0.25	4.2	2.7
CalCOFI F-47-117.35	8.2	4.2	2.9	1.1	1.3	1.0	1.5	2.5	1.1	0.52	4.8	3.0
CalCOFI F-46-130.40	8.5	4.7	3.2	1.2	1.7	1.0	1.6	3.0	1.3	0.80	4.9	3.2
CalCOFI 5303-123.40	9.0	5.0	3.2	1.1	1.7	1.0	1.6	2.8	1.2	0.65	5.4	3.2
CalCOFI 6604-133.40	9.2	5.3	3.4	1.1	1.5	1.1	1.8	3.1	1.4	0.89	5.4	3.6
CalCOFI C-46-117.40	9.5	5.2	3.6	1.3	1.7	1.2	1.7	3.1	1.5	1.1	5.6	3.6
CalCOFI 6605-123.70	9.7	5.4	3.5	1.2	1.7	1.2	1.8	3.2	1.6	1.1	5.8	3.7
CalCOFI F-46-133.35	10.0	6.2	3.7	1.2	1.9	1.3	1.8	3.5	1.8	1.2	6.4	3.8
CalCOFI 6004-130.45	10.3	6.3	3.8	1.4	2.0	1.3	1.8	3.5	1.7	1.2	6.5	4.4
CalCOFI F-46-133.35	11.2	6.8	3.8	1.4	2.2	1.3	1.8	4.0	2.1	1.5	7.0	3.8
CalCOFI 5304-123.40	12.0	7.7	4.5	1.4	2.5	1.5	1.8	4.2	2.4	1.8	7.7	5.2
CalCOFI 6605-127.45	15.0	9.4	5.8	1.7	3.2	1.9	2.1	5.2	3.5	3.1	9.7	5.4
SIO 65-201	15.4	9.3	5.8	1.7	3.0	1.8	2.2	5.5	4.0	2.9	9.6	5.8
CalCOFI 6604-133.30	15.9	10.0	6.5	2.1	--	2.0	1.9	5.2	3.6	2.8	10.1	7.1
*SIO 61-299	22.6	14.0	8.4	2.7	3.6	2.3	2.5	7.5	6.7	4.8	14.7	9.3
*SIO 54-87	27.8	18.6	10.6	3.1	4.5	2.8	3.0	8.9	8.8	6.2	19.3	11.2
*SIO 69-232	29.2	19.1	10.8	2.9	4.8	3.2	2.9	10.0	9.8	6.5	19.9	11.7
*LACM 8821-9	32.7	20.7	11.8	3.2	4.9	3.6	2.9	10.1	9.7	--	20.8	12.2
*LACM 8821-9	34.5	20.9	11.8	3.2	5.2	4.0	3.2	10.5	10.6	7.7	21.4	12.7
*LACM 8821-9	38.8	25.0	12.8	3.2	5 4	4.0	3.5	11.7	11.2	8.3	25.6	14.4
*LACM 8821-9	40.2	26.8	13.0	3.5	6.1	4.2	3.6	12.0	12.2	8.5	27.4	15.2
*LACM 8821-9	44.4	30.2	14.0	3.8	6.4	4.7	3.8	13.2	13.2	9.2	31.2	16.2

* Pelagic juvenile.

TABLE 2.—Meristics from cleared and stained larvae of *Sebastes macdonaldi*.

Length (mm)	Primary caudal fin rays		Secondary caudal		Branchiostegal rays		Pectoral fin rays		Hypural elements		Dentary teeth		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebral centra	Neural spines	Haemal spines
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Left	Right			Left	Right			
6.3	--	--	--	--	2	2	2	2	--	--	--	--	--	--	--	--	--	--	--
6.7	--	--	--	--	3	3	3	3	--	--	--	--	--	--	--	--	--	--	--
6.8	--	--	--	--	3	3	3	--	--	--	--	--	--	--	--	--	--	--	--
7.0	3	3	--	--	4	4	6	6	--	--	--	--	--	--	--	--	--	2	--
7.1	4	3	--	--	5	5	6	6	--	--	--	--	--	--	--	--	--	4	--
7.2	3	3	--	--	5	5	--	8	--	--	--	--	--	--	--	--	--	4	--
7.7	6	6	--	--	6	6	11	11	--	--	--	--	--	--	1-0	1-0	5	12	--
7.9	4	4	--	--	5	5	9	10	--	--	--	--	--	--	--	--	3	6	--
8.2	8	7	2	2	7	7	17	17	--	--	--	--	I,II-4	VII-0	1-3	1-3	24	20	7
8.5	7	7	--	1	6	6	15	15	1	1	--	--	--	--	1-3	1-3	18	18	6
8.7	8	7	--	1	7	7	16	16	--	--	--	--	--	IV-0	1-3	1-3	18	19	6
9.2	8	7	2	3	7	7	19	18	2	3	--	--	--	VII-8	1-4	1-4	23	21	9
9.4	8	7	4	4	7	7	19	19	2	3	--	--	III-7	XIII-13	1-5	1-5	24	23	13
9.7	8	7	3	4	7	7	19	19	2	3	--	--	III-7	XIII-13	1-5	1-5	24	23	12
10.0	8	7	5	6	7	7	19	19	2	3	4	5	III-7	XIII-13	1-5	1-5	26	24	14
10.3	8	7	5	5	7	7	19	20	2	3	4	4	III-7	XIII-13	1-5	1-5	26	24	14
11.3	8	7	4	4	7	7	19	19	2	3	5	5	III-7	XIII-13	1-5	1-5	26	24	14
12.0	8	7	8	7	7	7	19	19	2	2	3	2	III-7	XIII-13	1-5	1-5	26	24	14
15.0	8	7	10	11	7	7	19	19	3	2	11	13	III-7	XIII-13	1-5	1-5	26	25	14
15.9	8	7	10	11	7	7	19	19	3	2	12	10	III-6	XIII-12	1-5	1-5	26	25	14

The critical pelagic juvenile stages were found in the fish collections of the Scripps Institution of Oceanography (SIO) and the Los Angeles County Museum of Natural History (LACM). Demersal juveniles were obtained from bottom trawl collections of the Southwest Fisheries Center, La Jolla, and the University of California at Los Angeles (UCLA), in addition to the two sources mentioned above.

Prior to the completion of notochord flexion during caudal fin formation, the body length is defined as the distance from the tip of the snout to the posterior tip of the notochord. After notochord flexion is completed the usual standard length measurement, the distance from the tip of the snout to the posterior margin of the hypural plate, is used. Morphometric changes in rockfish can be conveniently grouped into three phases that correspond to the stages of notochord flexion—one before flexion, one during flexion, and one after flexion is completed. These stages are separated in the morphometric table. Other terms used in this table are defined as follows:

Snout-anus distance = distance along midline of body from tip of snout to vertical from anus

Head length = distance from tip of snout to cleithrum

Snout length = distance from tip of snout to anterior margin of eye

Upper jaw length = distance from tip of snout to vertical from posterior margin of maxillary

Interorbital distance = width of tissue dorsal to eyes

Body depth = body depth at base of pectoral fin

Pectoral fin length = maximum length of rayed portion of fin

Pelvic fin length = maximum length of rayed portion of fin

Snout to origin of anal fin = distance along midline of body from tip of snout to a vertical from anterior end of anal fin

Snout to origin of pelvic fins = distance along midline of body from tip of snout to a vertical from pelvic fin base.

Terms used in the description of larval osteology conform largely to those used in recent studies of the osteology of adult teleosts (e.g., Harrington, 1955; Weitzman, 1962; Topp and Cole, 1968).

DESCRIPTION OF DEVELOPMENT

DISTINGUISHING FEATURES

Early-stage larvae of *S. macdonaldi* are characterized by a low number of melanophores (average of eight) in the series along the ventral midline of the tail. Of the 27 other species illustrated in the literature, only *S. paucispinis* larvae, with an average of nine melanophores in this series, approaches the low number of *S. macdonaldi*. Early larvae of *S. macdonaldi* are also characterized by their small, densely pigmented pectoral fins. Melanophores cover completely the blade of the fin, but are restricted to the inner surface of the fin base. Also characteristic is the series of melanophores which extends from the nape to the pectoral fin base. Such melanophores are not present on any other of the 27 other eastern Pacific species illustrated to date.

A fourth character of limited utility is the absence of melanophores on the dorsal surface of the tail. *S. macdonaldi* is one of the 16 eastern Pacific species illustrated to date which lacks this pigment, and can be immediately separated from the 12 species in which it is present. This character should be used with caution because the dorsal series of melanophores forms later than the ventral series, at about the time of yolk depletion (Moser, 1967; Waldron, 1968). Thus, prolarvae collected prematurely from the ovaries may not have yet developed their dorsal pigment series, and illustrations of this stage are not strictly comparable with those of larvae cultured to the point of yolk depletion.

GENERAL MORPHOLOGY

Larvae of *S. macdonaldi* are similar in general appearance to those of *S. paucispinis* (Moser, 1967). Larvae hatch within the ovaries at a length of 4 to 5 mm, and then are extruded from the female. Newborn larvae have large heads with well-formed eyes and functional jaws (Figure 1A). The gut is short and bulbous; usually remnants of the yolk and oil globule are visible anteriorally in the region of the liver.

Relative body depth increases markedly during early larval stages and less so during later larval stages (Figures 1, 2). Body depth at the base of the pectoral fins averages 23% of the body length before notochord flexion, 33% during flexion, and 34% after flexion. In pelagic juveniles (Figure 3), relative body depth decreases slightly to about 30% in individuals 35 to 40 mm long. *S. paucispinis* is more slender throughout the larval and early juvenile stages; body depth averages 20% of the body length before notochord flexion, 24% during flexion, 31% following flexion, and 28% in pelagic juveniles.

Relative gut length increases gradually throughout the larval period. Accordingly, snout-anus length averages 42% of the body length before notochord flexion, 52% during flexion, 60% after flexion, 64% in pelagic juveniles. A similar gradual increase occurs in *S. paucispinis* (41, 44, 56, and 63% in the respective stages).

Relative head length increases slightly during the larval period; head length averages 28% of the body length before notochord flexion and 37% during and after flexion, but decreases during transformation and is 32% in the largest pelagic juveniles. Eye diameter averages 33% of the head length throughout the larval period and shows no trend of relative increase or decrease. Relative eye diameter decreases slightly to about 28% in transforming individuals, but increases to about 32% in the largest pelagic juveniles.

Upper jaw length is variable with respect to head length, probably because of the difficulty in obtaining uniform measurements from specimens with partially opened jaws. There is, however, a general trend of relative increase; jaw length averages 47% of head length before notochord flexion, 49% during flexion, and 52% in postflexion larvae. In large larvae and in pelagic juveniles the end of the maxillary is located beneath the middle of the orbit. With continued elongation of the maxillary in demer-

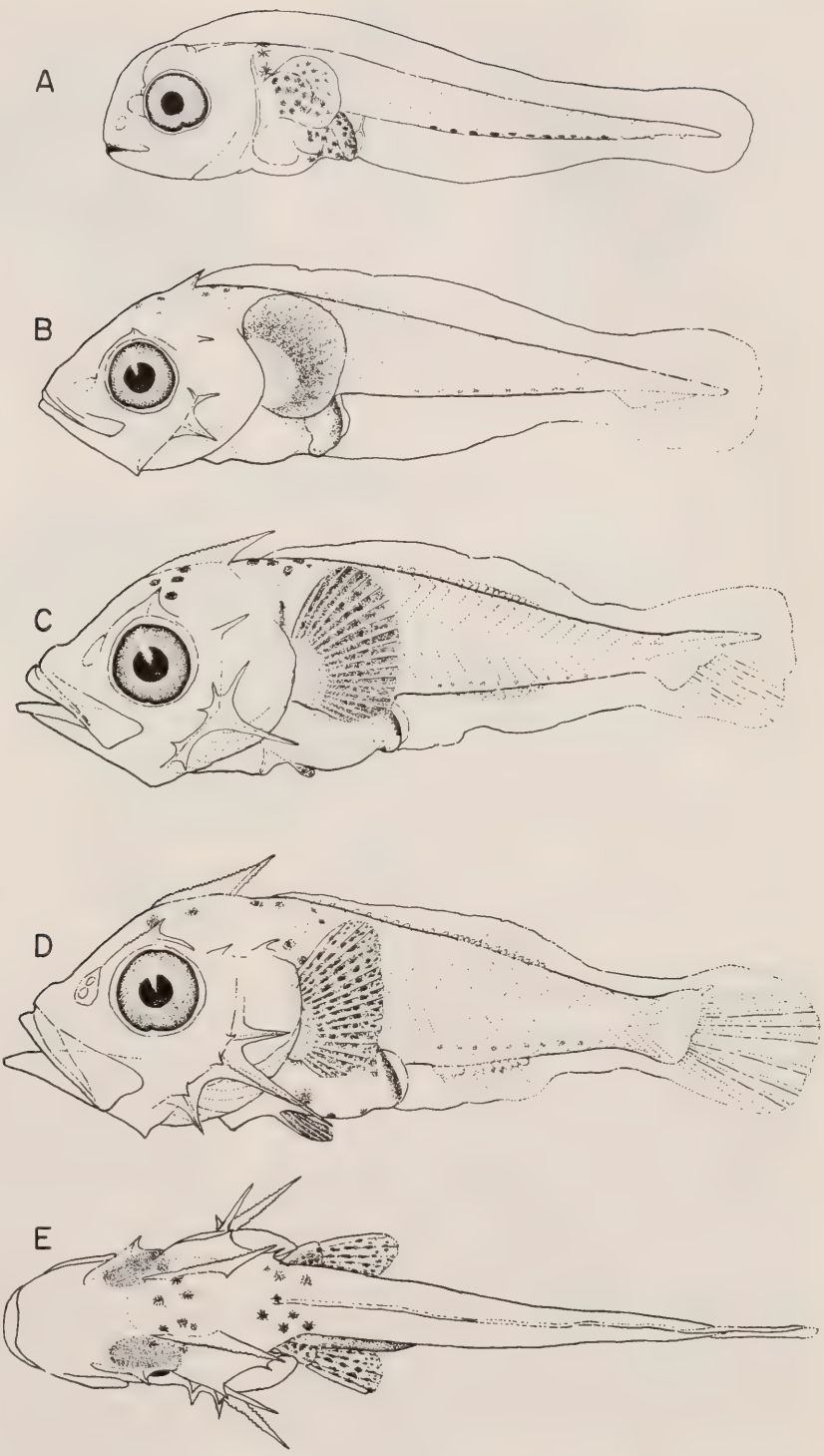

FIGURE 1.—Larvae of *Sebastes macdonaldi* from a pregnant female (A) and from California Cooperative Oceanic Fisheries Investigations (CalCOFI) plankton samples (B-E). A. 4.5 mm; B. 6.3 mm; C. 7.7 mm; D. 9.0 mm; E. dorsal view, 9.0 mm.

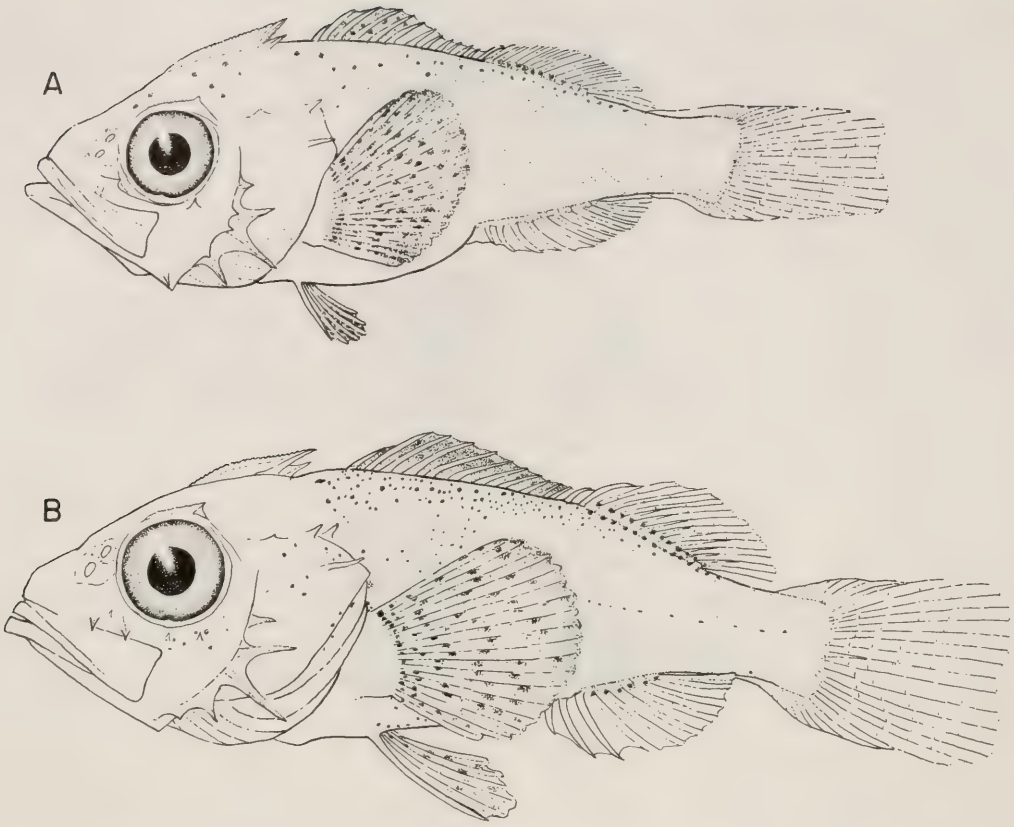

FIGURE 2.—Planktonic larvae of *Sebastes macdonaldi* from CalCOFI plankton samples. A. 11.2 mm; B. 15.9 mm.

sal juveniles (Figure 4) and in adults, its posterior end extends to below the posterior margin of the orbit. The relative length of the snout does not change markedly during the larval period; snout length averages 32% of the head length throughout the larval period. In pelagic juveniles snout length is reduced slightly to an average of 28% of the head length. Likewise, the width of the interorbital region changes little relative to head length in larvae; it averages about 46% of the head length. At the end of the larval period the interorbital distance becomes markedly narrower and averages 27% of the head length in pelagic juveniles. Similar changes in relative growth rate of the head, eyes, jaws, snout, and interorbital region occur in larvae and early juveniles of *S. paucispinis*.

FIN DEVELOPMENT

The pectoral fins begin to form during embryogenesis and, at parturition, the muscular base of each fin is distinct from the fan-shaped future rayed portion. The rayed portion enlarges considerably during early planktonic life and becomes covered solidly with melanophores (Figure 1B). The rays begin to ossify in larvae as small as 6.3 mm (Table 2); ossification begins with the most dorsal rays and then proceeds ventrad sequentially. Larvae 19.2 mm and larger have the full complement of 19 stained pectoral rays. The pectoral fins elongate slowly and gradually and have a short stubby appearance during most of the larval period. The length of the rayed portion of the fin averages 8% of

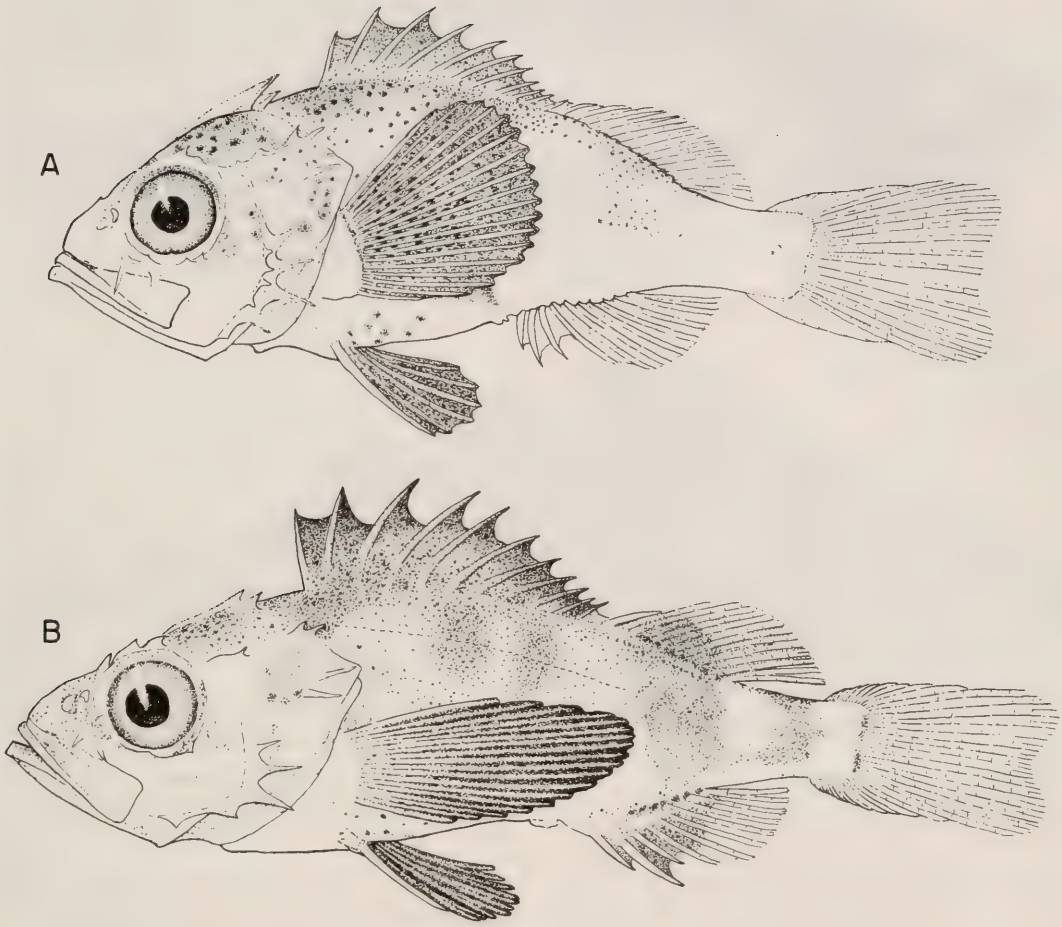

FIGURE 3.—Pelagic juveniles of *Sebastes macdonaldi*. A. A 15.4-mm transforming specimen (SIO 65-201, midwater trawl) which is just beginning to develop its juvenile melanophore pattern. Note that it is further advanced than the 15.9-specimen in Figure 2. B. A 29.2-mm specimen dipnetted on surface at night (SIO 69-232).

the body length in the stages before notochord flexion, 13% during flexion, and 19% in the stages following flexion. The fin elongates markedly in pelagic juveniles in which its average length is 31% of the body length (Figures 3B, 4A). This sequence of gradual elongation of the pectoral fins throughout the larval and early juvenile period contrasts with that observed in *S. paucispinis* (Moser, 1967). In that species, the maximum length of the pectoral fins, 40% of the body length, is achieved in 13-mm larvae and, thereafter, the pectoral fin length decreases relative to body length; pectoral fin length is 25% of the body length in newly transformed juveniles of *S. paucispinis*. In both species, the heavily pigmented pectoral fins are the most striking features of larvae and early juveniles.

The pelvic-fin buds appear early, in larvae as small as 6.3 mm, and become covered with melanophores. The rays begin to differentiate in 7-mm larvae. Ossification of the spines is visible initially in a 7.7-mm specimen in the stained series (Table 2). Ossification of the rays proceeds sequentially posteriad from the spines; the

FIGURE 4.—Juveniles of *Sebastes macdonaldi*. A. A 40.2-mm pelagic juvenile (LACM 8821-9) collected by midwater trawl in the Gulf of California. B. A 62.1-mm demersal juvenile (SIO 65-227) collected by otter trawl near Point Tosco, Baja California.

full complement of five ossified rays is present in each fin in a 9.4-mm stained specimen. Like the pectoral fins, the densely pigmented pelvics elongate gradually throughout the larval period. Pelvic fin length increases from 4% of the body length at the initiation of notochord flexion to 10% at its completion. Following flexion, it increases gradually to a maximum of 18 to 21% of the body length in larvae 15.0 to 16.0 mm long. In pelagic juveniles pelvic fin length is 21 to 22% of the body length.

The caudal-fin anlage first appears in larvae about 5.0 mm long as a ventral thickening near the tip of the notochord. The cartilaginous hypural elements begin to differentiate when the larvae are about 6.0 mm (Figure 1B) and the maximum number of three superior and two inferior hypurals is present at about 8.0 mm. Ossification of these elements begins in larvae about 8.5 mm long and all hypurals, except the slender dorsal-most element of the superior series, are ossifying in a larva 9.2 mm long. Fusion accompanies further ossification in the superior series; in the largest larva the two larger superior elements have nearly fused into a single plate, while the slender uppermost element remains separate and has just started to ossify. In the inferior series the larger upper element has two centers of ossification which produce a solid calcified plate in the largest larva. The slender lowermost element is also well ossified but remains separate. Thus, larvae of 15-mm length have achieved the adult complement of two superior and two inferior hypurals. The principal caudal rays begin to ossify in 7-mm larvae (Table 2). Ossification proceeds dorsad in the superior series, above the midline of the fin, and ventrad in the inferior series; the adult complement of

8 + 7 principal rays is present in an 8.2-mm larva of the stained series. Also, the initial procurrent rays are ossifying in this specimen. Ossification of these rays proceeds anteriad in both superior and inferior series. The largest larva (15.9 mm) has 10 superior and 11 inferior ossified rays, but the full complement of 11 to 13 superior and 13 to 15 inferior rays is attained in pelagic juveniles.

The dorsal and anal fins are the last to appear. The bases of the fins appear in larvae 5.3 to 7.0 mm long (Figures 1B, C). Cartilaginous radial elements start to differentiate when the larvae are about 7.0 mm and the full complements of these elements are present in larvae 8.0 to 8.5 mm. Initial ossification of the spinous rays of these fins is visible in an 8.2-mm specimen in which the three anal spines and the anterior seven dorsal spines are stained. A larger, but apparently less advanced specimen, 8.7 mm long has only four stained dorsal spines and shows no stain on the anal spines. A 9.2-mm faintly stained larva has seven spinous and eight soft dorsal rays but shows no stain on the anal rays. The next larva in the stained series, 9.4 mm long, has the adult complement of III-7 anal and XIII-13 dorsal rays. The remaining larvae in the stained series, with the exception of one specimen, also have III-7 anal and XIII-13 dorsal rays.

PIGMENTATION

Newly hatched *S. macdonaldi* larvae have a melanophore pattern similar to that of *S. paucispinis*. The gut is covered with a mantle of melanophores that is solid on the dorsal surface and more sparsely distributed on the lateral and ventral surfaces (Figure 1A). A line of melanistic dashes on the ventral midline of the tail extends posteriad from the third or fourth postanal myomere. In a sample of 60 newborn larvae of *S. macdonaldi* the number of melanophores in the ventral midline series ranged from 6 to 14 with a median of 8. Thus, this species has fewer ventral midline melanophores than any eastern Pacific species of *Sebastes* studied to date (see Morris, 1956; DeLacy et al., 1964; Moser, 1967). Head pigmentation in newborn larvae consists of a series of melanophores that line the anterior region of the lower jaw and one to several melanophores that form a blotch on the nape. The pectoral fins also are pigmented; the inner surface of each fin base is covered solidly with melanophores while the lateral surface is pigmentless. The future rayed portion of the fin has sparsely distributed melanophores on both lateral and inner surfaces.

Melanophores are added throughout the larval period so that large larvae of *S. macdonaldi* are among the most heavily pigmented of all rockfish species (Figures 1, 2, 3). Much of the melanistic pigment is added in the head region. One or two melanophores appear over each optic lobe of the brain in 4- to 5-mm larvae. Similarly one or two melanophores appear above each side of the cerebellum in larvae of the same size. Melanophores are added continuously to the dorsal surface of the brain so that it is covered completely when the larvae reach 8.0 mm. Beginning in larvae about 7.0 mm long, isolated melanophores form anterior to the cleithra and eventually form a small patch that is covered by the opercle. When the larvae reach about 10.0 mm, considerably more pigment is added to the head. Patches of melanophores form around the external nares and along the anterior rim of the upper jaw; gradually the entire dorsal region of the snout becomes covered. Also, a conspicuous melanophore patch appears at the ventroposterior margin of the orbit and on the dorsal surface of the opercle.

Pigmentation on the gut, particularly on the dorsal and lateral surfaces, becomes more extensive during larval development. Beginning in larvae of about 5.0-mm length, melanophores are added in the region dorsal to the pectoral fin base and eventually a continuous band of melanophores extends from the gut to the enlarging melanistic blotch at the nape.

The number of melanophores in the series at the ventral midline of the tail appears to diminish as development proceeds; this may be an apparent reduction since the melanophores become embedded in the developing hypaxial musculature and later become obscured by the developing anal fin. Typically, in larvae larger than 8.0 mm the three posterior melanophores

in the series are visible along the ventral margin of the caudal peduncle while more anterior melanophores of the series are barely visible above the developing anal fin.

The paired fins are strikingly pigmented. Melanophores are added continuously to the rayed portion of the pectoral fin but are scattered until the larvae are about 7.0 mm long (Figure 1C) when they become concentrated on the membranous portions of the fins between the developing rays and give the fins a striated appearance that remains throughout the larval period. The base of the pectoral fin remains heavily pigmented only on the medial surface. Melanophores begin to appear on the pelvic fins in larvae about 7.0 mm long and form a striated pattern like the pectorals when the larvae reach a length of about 8.5 mm.

The median fins develop pigmentation considerably later in the larval period. When larvae reach about 9.0-mm length (Figures 1D, E), the melanophore patch on the nape begins to expand posteriad along the dorsal midline to form an elongated patch at the base of the spinous dorsal fin. A separate elongated patch of melanophores develops at the base of the soft dorsal fin and the two become connected by a narrow bridge of melanophores when the larvae reach about 10.0 mm. Melanophores begin to form on the anterior portion of the spinous dorsal fin when the larvae are about 9.0 mm long. Gradually the pigmented area of the fin enlarges until the entire spinous dorsal is pigmented in larvae longer than 15.0 mm (Figure 2B). Pigment on the soft dorsal fin is limited to a series of melanophores that covers the distal radial elements of the fin base. These melanophores begin to appear in 11-mm larvae and cover nearly all the radial elements when the larvae reach 15.0 mm (Figures 2A, B). A similar series of melanophores develops along the anal fin base when the larvae reach 12.0-mm length. One to several melanophores appear at the posterior margin of the hypural elements. In pelagic juveniles other melanophores are added here to form a vertical line (Figures 3B, 4A).

The beginnings of the juvenile pigment pattern appear in larvae 15.0 to 16.0 mm long when saddles of melanistic pigment start to develop ventrad from the elongate patches that lie along the dorsal fin base (Figures 2B, 3A). The first of these extends ventroanteriad from the origin of the dorsal fin to meet with the melanistic blotch on the opercle. A second saddle extends from the middle region of the spinous dorsal fin ventrad to overlie the lateral line, as does a third saddle which extends ventrad from the base of the soft dorsal fin.

These melanistic saddles become further developed in pelagic juveniles. In a 22.6-mm juvenile the pigment saddle at the soft dorsal fin extends almost to the base of the anal fin, and a fourth saddle is present at the caudal peduncle. In a 29.2-mm specimen (Figure 3B) the broad band at the soft dorsal is continuous and extends onto the rays of the dorsal and anal fins. The band at the caudal peduncle also extends to the ventral midline. Also, in this specimen, an additional saddle is present below the posterior end of the spinous dorsal fin, just posterior to the one located below the middle of the fin. In the largest pelagic juveniles (33-44 mm) the most anterior bar at the origin of the dorsal fin is obliterated as it becomes continuous with the solidly pigmented dorsal region of the head (Figure 4A). Melanistic pigment on the fins is augmented in pelagic juveniles. The entire spinous dorsal is dark and has a black margin whereas only the basal regions of the soft dorsal and anal fins are covered with melanophores. The caudal fin lacks melanophores. The pelvic fins remain pigmented as in late-stage larvae; however, a zone without melanophores develops on the basal third of each pectoral fin.

The melanistic pigment pattern of the smallest demersal juveniles (60 mm SL) remains essentially like that of pelagic juveniles (Figure 4). The smallest fresh specimens examined were 150 mm SL. In these the melanistic saddles and bands are separated by dusky areas above the horizontal septa. Below the septa, the background color is crimson, as is the lateral line and the head below the ventral markin of the orbit. The spinous dorsal fin is dusky with a black margin whereas the soft dorsal has a dusky base, a black central zone, and a pale margin. The caudal, anal, pelvic, and pectoral fins have crimson rays alternating with black between the rays.

In large adults the lateral melanistic patches and bands coalesce to form a solid black zone above the horizontal septa with a crimson zone below. At least the posterior half of the lateral line remains bordered by crimson. The spinous and soft dorsal fins become black. The caudal fin is black except for a vertical crimson zone at the base. The anal and ventral fins remain crimson with black between the rays. The pectoral fins become black except for a red zone at the proximal third of each fin.

SEQUENCE OF OSSIFICATION

The sequence of calcification of bones in larvae of *S. macdonaldi* is similar to that described for larvae of Myctophidae (Moser and Ahlstrom, 1970). As in myctophids, the maxillaries and cleithra are the first elements to ossify. In fact, the maxillaries, cleithra, and opercles are beginning to ossify in full-term intraovarian larvae. The sequence of ossification of other head, appendicular, and axial elements in a stained series of *S. macdonaldi* is shown in Table 3. For each element, the larval length at initial ossification and the larval length at which the element achieves its adult form are given. Selection of the point at which an element achieves its adult form, admittedly, is somewhat subjective since bone formation is a gradual process that continues throughout the life of the fish. In rockfish, as in most other teleosts, most of the skeletal elements become ossified during the larval period and assume a shape which, except for minor surface irregularities and processes, closely resembles that found in juveniles and adults. The branchial arches and cranial spines ossify gradually and generally have not achieved their adult form before the end of the larval period. For this reason these are listed in separate tables (Tables 4, 5), which give only the sequence of initial ossification.

Although the neurocranium is unossified in unborn larvae, the frontals, pterotics, and parasphenoid form soon after birth, in larvae 5.1 to 5.2 mm. These are followed by the parietals, exoccipital, bosioccipital, and supraoccipital, and later the circumorbital bones and the more interior neurocranial elements.

In the upper jaw the maxillaries begin to ossify before birth. These are followed by the main elements of the lower jaw, the dentaries and articulars, which begin to ossify at 5.1 to 5.2 mm. Other elements of the jaws, the premaxillaries and angulars, are beginning to ossify in a 6.3-mm stained larva. All elements of the mandibular arch achieve their adult form early in the larval period, between 7.0 and 8.5 mm. The elements of the palatine series are slower to ossify. The quadrates begin to ossify at about 6.3 mm and the others follow gradually; the last elements to initiate ossification, the palatines and metapterygoids, achieve their adult form in 12.0-mm and 15.9-mm larvae respectively.

The bones of the hyoid arch and opercular series initiate ossification gradually, beginning with the opercle in unborn larvae. The other bones of the opercular series have started to ossify before the larvae reach 6.3 mm, and all have achieved their adult form at 7.9 to 8.2 mm. Elements of the hyoid arch, particularly the ceratohyals and interhyals, are slower to initiate and complete ossification.

In the appendicular skeleton, the cleithra are the first bones to become ossified. They are heavily stained in unborn larvae and are the first skeletal elements to ossify. Following birth, the other bones of the pectoral girdle gradually initiate ossification. Among the last to appear are the four proximal radial elements, which ossify in a dorsal-to-ventral sequence. The coracoids and the single pair of extrascapulars initiate calcification at about 12.0 mm and are formed in the 15.9-mm specimen. The pelvic bones appear initially in a 9.2-mm stained specimen; through gradual ossification the pelvics become fused along their medial surfaces.

The paired neural arch elements are the first bones of the axial skeleton to ossify. At first only the most anterior pair is visible in a 7.0-mm larva, but gradually others are added in a posteriad sequence. When the larvae are about 8.0 mm long, the distal ends of each pair begin to fuse in the midline to complete the neural arch. This fusion and the resultant formation of a neural spine on each arch also occurs in an anterior to posterior sequence. The full complement of neural spines, including a shortened one

TABLE 3.—Sequence of ossification in larvae of *Sebastes macdonaldi*. The initial ossification of an element is indicated by "X" and the point of the arrow indicates the larval size at which the element achieves the general shape it will have in the juvenile and adult.

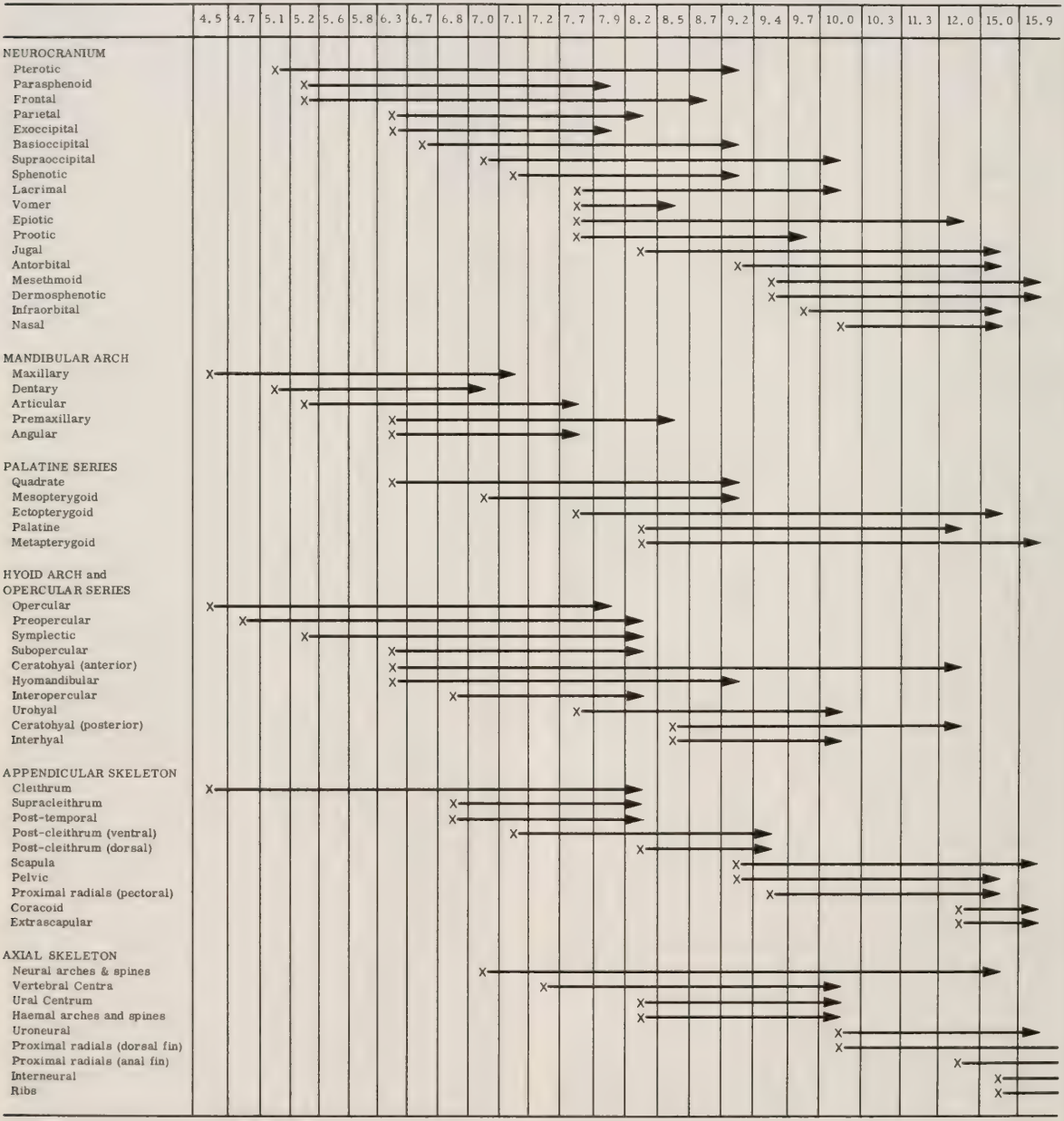

TABLE 4.—Sequence of initial ossification of branchial arch elements in larvae of *Sebastes macdonaldi*.

Element	Larval length at initial ossification (mm)
Pharyngobranchial teeth (3rd arch)	4.7
Ceratobranchial (1st arch)	6.3
Ceratobranchial (2nd arch)	6.3
Ceratobranchial (3rd arch)	6.3
Ceratobranchial (4th arch)	6.7
Ceratobranchial gill rakers (1st arch)	6.7
Ceratobranchial gill rakers (2nd arch)	7.2
Epibranchial (1st arch)	7.2
Epibranchial (2nd arch)	7.2
Ceratobranchial teeth (5th arch)	7.2
Ceratobranchial (5th arch)	7.7
Epibranchial (3rd arch)	7.7
Pharyngobranchial teeth (4th arch)	7.7
Ceratobranchial gill rakers (3rd arch)	7.7
Epibranchial gill rakers (1st arch)	8.2
Epibranchial (4th arch)	8.2
Hypobranchial (1st arch)	8.7
Epibranchial gill rakers (2nd arch)	8.7
Basibranchials	9.2
Hypobranchial (2nd arch)	9.2
Hypobranchial (3rd arch)	9.4

TABLE 5.—Sequence of initial ossification of head spines of larvae of *Sebastes macdonaldi*.

Spine	Element	Size of specimen at initial appearance (mm)
Pterotic	Pterotic	5.1
Preopercular, 3rd, posterior series	Preopercular	5.1
Preopercular, 4th, posterior series	Preopercular	5.2
Parietal	Parietal	6.3
Postocular	Frontal	6.3
Preopercular, 1st, anterior series	Preopercular	6.3
Preopercular, 2nd, anterior series	Preopercular	6.3
Preopercuiar, 3rd, anterior series	Preopercular	6.3
Preopercular, 2nd, posterior series	Preopercular	6.7
Supracleithral	Postemporal	7.7
Suborbital, 1st, inferior series	Lacrimal	8.2
Suborbital, 1st, superior series	Lacrimal	8.2
Preopercular, 1st, posterior series	Preopercular	8.2
Nuchal	Parietal	8.2
Opercular, 1st	Opercle	8.2
Opercular, 2nd	Opercle	8.2
Preopercular, 5th, posterior series	Preopercular	9.4
Suborbital, 3rd, superior series	Jugal	9.4
Cleithral	Supracleithrum	12.0
Nasal	Nasal	15.0
Suborbital, 2nd, inferior series	Lacrimal	15.0
Suborbital, 2nd, superior series	Infraorbital	15.0
Preocular	Antorbital	22.6
Supraocular	Frontal	22.6
Tympanic	Frontal	22.6

on the ultimate preterminal vertebra, is present in a 15.0-mm stained specimen.

The next elements of the axial skeleton to appear are the vertebral centra. The most anterior centra begin to ossify in larvae about 7.2 mm long. Ossification within each centrum begins at the bases of the neural arch and spreads mesially to form a straplike bridge between the bases. A similar structure forms ventrally between the bases of the haemal arch and ultimately the two bridges are joined by lateral ossification, to produce a complete central ring. This process proceeds in a posteriad sequence until the full complement of 25 central rings is attained in larvae of about 10.0 mm. Ossification of the ural centrum begins in an 8.2-mm specimen with the formation of two tandem osseus plates on each lateral surface. These spread rapidly to cover the entire lateral and dorsal surface of the centrum. Ossification of two ventral unossified regions is completed at about 10.0 mm to coincide with the formation of the ultimate preterminal centrum.

Haemal arches begin to ossify at about 8.2-mm length in a manner similar to that of the neural arches. Closure of the haemal processes into arches and the formation of haemal spines proceeds posteriad sequentially; when completed at 10.0 mm, vertebrae 1 to 4 are without haemal processes, 5 to 9 have unfused haemal processes, 10 and 11 have haemal arches without spines, and 12 to 25 have arches and spines.

All of the remaining major axial elements begin to ossify in larvae 10.0 mm or longer. The uroneurals appear as a pair of slender elements above the terminal centrum in a 10.0-mm specimen; they remain paired and sliverlike throughout the larval period. The proximal radial elements of the dorsal fin also begin to ossify at 10.0 mm and those of the anal fin at 12.0 mm, both in a posteriad direction; neither series is completed by 15.9 mm. A single interneural appears slightly above and in advance of the first neural spine in a 15.0-mm larva. Also, in this specimen the most anterior few ribs have just begun to ossify.

Several generalizations can be made from the information listed in Table 3. It is obvious that the various skeletal elements begin to ossify over a wide range of larval sizes and that the elements vary greatly in the time required for each to attain its adult form. For example, in the neurocranium, the jugal (third circumorbital) is formed over a span of nearly 7.0-mm length (8.2-15.0 mm) while the vomer begins to ossify

and achieves its adult shape over a span of about 1.0 mm (7.7-8.5 mm). Similar variation is found in the mandibular, palatine, and hyoid arches and in the axial and appendicular skeletons. Another less obvious generalization from Table 3 is that functionally related contiguous elements tend to achieve their adult form at about the same larval stage, regardless of when they underwent initial ossification. For example, the first six bones listed in the table are the major elements of the roof, sides, and floor of the brain case. Although they undergo initial ossification in a gradual sequence, all achieve their adult form in larvae 7.9 to 9.2 mm long. The bones of the opercular series (opercular, preopercular, subopercular, interopercular) begin to ossify in successive stages, but all achieve adult form at about the same stage. The pectoral girdle provides two excellent examples of this tendency in the cleithrum-supracleithrum-postemporal series and the scapula-proximal radial-coracoid series. Finally, there is no correlation between sequence of ossification and the origin (endochondral or dermal) of a bony element. Thus, of the first six elements of the neurocranium mentioned above, half are endochondral and half are dermal in origin. Here, the early appearance of these elements appears to be related to function and not to the kind of bone formed.

Analysis of the sequence of ossification of branchial elements is difficult since ossification is so gradual that one cannot choose a larval stage at which a given element achieves its basic adult form. Accordingly, only the larval size at which an element begins to ossify is listed in Table 4. As in other teleosts examined by me, the first bony structures to ossify in the larvae are the pharyngobranchial teeth. In *S. macdonaldi*, the tooth patches of the third pair of pharyngobranchial elements appear in the smallest planktonic larvae and enlarge throughout the larval period. In larvae of the Myctophidae it is the tooth patches of the fourth pharyngobranchials which ossify first (Moser and Ahlstrom, 1970). Aside from this, the sequence of ossification is similar in *Sebastes* and Myctophidae. The ceratobranchials are the first elements of the arches to ossify. These are followed by the epibranchials and hypobranchials, generally in an anterior to posterior sequence, beginning with those of the first arch. The first gill rakers to form are those on the first pairs of ceratobranchials and epibranchials and, gradually, they appear on more posterior arches. Within each arch, ossification proceeds outward from the angle of the arch. The full complement of rakers on the first arch is not achieved during the larval period.

Head spines present a special problem since some of the spines formed during the larval period are not found in adults. The terminology of Phillips (1957) is used in the discussion that follows. The first spines to form on the neurocranium are on the pterotic bones (Table 5). Interestingly, these spines begin to ossify before the bones themselves, and ossification of the bones spreads outward from the base of each spine. The spines are at first acute, but broaden during the larval period to produce a pterotic shelf in the largest larvae. The spine and shelf become reduced in pelagic juveniles and are absent in demersal juveniles and in adults. The two other pairs of spines which develop early in the larval period are the parietals and postoculars. The paired parietal spines develop as the terminal points of a pair of serrated parietal ridges and attain their maximum relative length (20-23% of the head length) in larvae 8.0 to 10.0 mm long. The ridges and their spines become reduced during later larval stages but remain in juveniles and adults. The postoculars develop from lateral shelves of the frontal bones that project over the eyes. Initially the spines are positioned directly above the eyes but gradually shift posteriad to their adult position. Preocular, supraocular, and tympanic spines do not form during the larval period; they are beginning to form in a pelagic juvenile 22.6 mm long and are well formed in the largest pelagic juveniles.

Other prominent cranial spines which develop later in the larval period are the suborbitals, nuchals, and nasals (Table 5). The suborbital spines form in two series: one series of ventrally directed spines develops on the ventral margin of each lacrimal (first circumorbital) bone and another series of laterally directed spines forms directly below the orbit. This lat-

ter series, composed of a single spine on each lacrimal, infraorbital, and jugal element, forms a shelf in late-stage larvae and in juveniles, but usually only the lacrimal spine remains in adults. The inferior series persists in adults and typically contains 3 to 5 spines. A nuchal spine forms directly posterior to each parietal spine in larvae about 8.0 mm long and persists in juveniles and adults. Nasal spines are late to form (15.0 mm) but also persist in adults.

Two spines appear on each preopercle in larvae 5.1 to 5.2 mm long. These are the third and fourth members of a series of five preopercular spines that forms throughout the larval period (Table 5). The third preopercular spines develop three longitudinal serrated ridges and elongate rapidly to become the longest larval spines. They reach a maximum length of 35% of the head length in larvae about 9.0 mm long and then decline in relative length. The five preopercular spines remain in juveniles and adults, but the short spines which develop immediately anterior to the second, third, and fourth preoperculars (Table 5) become obsolescent after the larval period. A pair of spines forms at the posterior margin of each opercle and persists in juveniles and adults.

The supracleithral and cleithral spines develop during the larval period; the supracleithral spines form on the postemporal elements in larvae about 7.7 mm long and the cleithral spines form on the supercleithra at about 12.0 mm. Both pairs persist into the adult stage.

DISTRIBUTION

S. macdonaldi has the most southerly distribution of any species of *Sebastes* in the eastern north Pacific. Chen (1971) lists its southern range record as Morgan Bank off Baja California (lat 23°24.0′N, long 111°11.5′W) and reports on the capture of a single adult specimen (LACM 8837-4) from Santa Inez Bay in the Gulf of California (lat 26°59.1′N, long 111°48.9′W). A collection of six pelagic juveniles (32.7-44.4 mm SL; LACM 8821-9) by midwater trawl from the Ballenas Channel in the Gulf of California (lat 28°56.5′N, long 113°10.5′W) is reported herein. Although the localities at Morgan Bank and Santa Inez Bay are separated by a distance of approximately 1,000 km, it is likely that future collections in this region will substantiate Chen's (1971) suggestion that the outer coast and Gulf of California populations are continuous.

The southerly distribution of *S. macdonaldi* is shown by the distribution of the larvae (Table 6, Figure 5). For the 4 years examined, larvae were taken as far north as CalCOFI line 90 and as far south as line 137. Line 90, running southwesterly from Dana Point, Calif., probably delimits the northern extent of reproduction for this species, although an adult has been taken as far north as Pt. Sur, Calif. (Phillips, 1961). Total numbers of larvae and frequency of occurrence of larvae increase to the south of line 90.

FIGURE 5.—Stations at which larvae of *Sebastes macdonaldi* were collected during 4 years (1953, 1960, 1965, and 1966) of CalCOFI plankton surveys. Solid circles indicate stations where number of *Sebastes macdonaldi* larvae exceeded mean number (4.8) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom, 1961, for complete grid).

TABLE 6.—Total numbers of *Sebastes macdonaldi* larvae taken on 14 CalCOFI lines for 4 years (1953, 1960, 1965, and 1966) and abundance of larvae of this species compared with the total numbers of *Sebastes* larvae taken in hauls containing *S. macdonaldi*.

CalCOFI line	Latitude[1]	Total number stations occupied	Total stations containing *S. macdonaldi*	Percentage of positive stations to total stations	Number of *S. macdonaldi* larvae	Total number of *Sebastes* larvae in hauls containing *S. macdonaldi*	Percentage *S. macdonaldi* larvae of total *Sebastes* larvae in hauls positive for *S. macdonaldi*
90	33°28.5′	383	1	0.26	1	31	3
93	32°56.0′	380	1	0.26	1	4	25
97	32°17.5′	325	1	0.31	1	28	4
103	31°07.0′	283	4	1.41	9	226	4
107	30°27.9′	273	8	2.93	12	226	5
110	29°52.0′	306	9	2.94	17	202	8
113	29°24.2′	283	19	6.71	47	285	16
117	28°58.0′	315	47	14.92	289	968	30
120	28°25.0′	365	33	9.04	110	332	33
123	27°26.2′	198	28	14.14	151	613	25
127	26°57.5′	202	33	16.34	143	252	57
130	26°33.5′	243	22	9.05	37	100	37
133	26°08.5′	209	23	11.00	207	224	92
137	25°36.1′	214	15	7.01	39	45	87

[1] Latitude of most shoreward station of each CalCOFI line.

They attain their largest numbers from line 117 to line 127 (Cedros Island to San Hipolito Point) and then decrease to line 137. In contrast, for those hauls containing *S. macdonaldi*, the ratio of this species to the total number of *Sebastes* larvae in these hauls increases continuously southward. *Sebastes* larvae were not taken on lines south of 137, probably because of the infrequent occupancy of these lines. Reproduction of *S. macdonaldi* occurs as far south as Morgan Bank (between lines 147 and 150), since one of the two specimens collected there was a term female with viable larvae.

The seasonal abundance and size of *S. macdonaldi* larvae at all CalCOFI stations during 1953 and 1960 are shown in Table 7. Larvae began to appear in January, increased in numbers in February, and reached a peak in March. Abundance declined progressively from April to June. The mean length of the larvae increased slightly during the 6-month period and the largest larvae were collected from March to June.

The larval stage is ended at about 16 mm; indeed, a 15.4-mm specimen is already beginning to develop the juvenile melanophore pattern and the juvenile arrangement of cranial spines. The pelagic juveniles are rare in plankton collections, probably because of their ability to avoid plankton nets. Also, they may occur deeper than 140 m, the usual maximum depth of CalCOFI plankton tows. Nevertheless, a number of pelagic juveniles, 22.6 to 44.4 mm long, were captured by plankton net, midwater trawl, and dip net. These are listed in Table 1 and discussed in the previous section of the paper. The smallest juvenile collected by bottom trawl was 59.3 mm. This suggests that the transition from pelagic to demersal habitat occurs in the size range of about 45 to 60 mm. Demersal juveniles 60 to 100 mm are captured typically at a depth range of 80 to 100 m. With further growth they appear to seek deeper habitats as there is a trend for larger fish to be collected from greater depths. The largest specimen examined (532

TABLE 7.—Numbers (A), mean length in mm (B), and size range in mm (C) of *Sebastes macdonaldi* larvae taken during 2 years of the California Cooperative Oceanic Fisheries Investigations (CalCOFI).

Year	CalCOFI lines	JANUARY			FEBRUARY			MARCH			APRIL			MAY			JUNE		
		A	B	C	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
1953	97-107	2	4.2	4.2	4	4.2	4.2-4.3	0	0	0	1	4.8	4.8	0	0	0	0	0	0
	110-120	5	4.3	3.8-5.3	19	4.5	3.5-7.1	138	5.0	3.3- 9.5	26	6.2	3.7-10.0	4	4.8	3.8-6.2	0	0	0
	123-137	13	4.4	3.3-3.5	20	4.6	3.9-8.7	143	4.8	3.3-11.2	34	5.3	3.8- 8.8	5	5.4	3.3-9.6	0	0	0
1960	97-107	0	0	0	6	5.1	4.3-6.5	6	5.6	4.7- 8.2	2	4.9	4.9	0	0	0	0	0	0
	110-120	0	0	0	12	4.7	4.4-5.2	81	5.2	3.8- 8.8	25	4.8	4.0- 6.2	4	5.3	4.5-7.3	5	4.3	3.7-5.8
	123-137	1	4.2	4.2	14	4.9	4.0-5.8	184	4.7	3.4-10.8	76	5.2	3.2-10.3	17	5.1	4.1-9.6	1	6.0	6.0

mm SL, SIO 65-126) was taken by hook and line at 256 m.

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CYCLING OF ELEMENTS IN ESTUARIES

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ABSTRACT

Meaningful evaluation of the ecological stresses imposed by man's release of heavy metals or radioisotopes into estuaries requires an improved understanding of the interactions between the waste materials and the functional components of the ecosystem. In this paper, we review and discuss the types of information required for the development of useful models for the cycling of contaminant metals (both radioactive and stable) in estuarine ecosystems. With particular reference to the coastal plain estuaries of the southeastern United States, we discuss the major reservoirs of those metals, the mechanisms and pathways of elemental transformation and rates of elemental turnover among reservoirs, and the responses of these processes and reservoirs to environmental change. A conceptual systems model is presented as the preliminary phase in the development of dynamic mathematical models of elemental cycling.

Estuaries form the interface between the open ocean and man's land base, which in the coastal zone undergoes intensive development to facilitate maximum use of the sea. This narrow interface is a highly productive environment used at some stage of development by most of the marine fishery organisms exploited by man. Waste products of man's expanding population and increasing industrialization are transported into and through this estuarine environment and may render the habitat unsuitable for desirable species, or may render certain species unfit for human consumption. Man's impingement upon estuaries has assumed many forms; estuarine habitats have already succumbed to industrial and municipal pollution, to landfill and dredging operations; and economic and population pressures demand that additional estuarine areas be challenged by an increasing multiplicity of additions and modifications whose combined ecological effects are yet unknown.

Meaningful evaluation of the ecological stresses imposed by man's activities requires an improved understanding of the interactions between the wastes and the functional components of the ecosystem. Such understanding entails knowledge of the general principles of ecosystem operation, and not merely a description of the ecosystem structure at one or more instants in time. Man's continued and expanding variety of demands on estuarine environments as producers of food, avenues of transportation, receptacles for wastes, and as sources of recreational and esthetic pleasure make it imperative that we understand the interactions of all the material imports, whether of human or natural origin; and all the outputs, including both tidal exports and human exploitation of resources, to ensure the continued viability of the resultant ecosystems. No estuarine ecosystem has yet been studied in sufficient detail to permit accurate prediction of ecosystem response to contaminative additions. Considerable insight may be gained, however, from attempts to synthesize adequate predictive systems models from fragmentary data already available from ecological studies, experimental biology, and experience with previous instances of pollution. In this paper, we examine and discuss briefly the nature of the information required for the development of useful models for the cycling of contaminant metals (both radioactive and stable isotopes) in estuarine ecosystems.

To understand the "cycling of elements" in a natural ecosystem necessitates identifying the major reservoirs of those elements, determining

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the mechanisms and pathways of elemental transformations and rates of elemental turnover among reservoirs, and determining the response of these processes and reservoirs to changes in the environment under study.

In aquatic ecosystems, nearly all of the metallic elemental content of the system resides in the sediments and in the water. The fraction residing in the biota is small—with phytoplankton and zooplankton constituting the most important living elemental reservoirs in terms of turnover and total physical transport and redistribution processes. The major commercial species harvested by man from estuaries have little effect on the overall distribution of metallic elements in the estuary, simply because most of these species are high in the trophic scheme and have relatively low biomass. Yet, in contaminated environments these same species may concentrate certain elements to levels potentially harmful to people consuming large quantities of seafood. Our consideration of elemental cycling must therefore be biased toward biological species of little importance to the overall elemental mass balance because these species form the major interface between man and the remainder of the ecosystem.

METALLIC ELEMENTS OF PRIMARY CONCERN

In the preceding and ensuing paragraphs we discuss the cycling of "metallic elements." Such a generalization is not entirely practical because chemical and physical characteristics of the different metals determine to some extent their behavior in the natural environment and their relative toxicity to biological systems influences the extent of our interest in the various metals. In addition, the relative abundance of various elements affects both their ecological behavior and human interest. In terms of chemical and physical properties, we can categorize the metals into five groups: alkali metals, alkaline earths, transition elements, rare earths, and actinide elements. The transition elements may be further subdivided into "family groups" on the basis of the electronic configurations of the atoms. The term "heavy metal" usually refers to all those metals with atomic numbers higher than 20 (Ca), i.e., beginning with the first transition series: Sc, Ti, V, Cr, etc. In the popular literature "heavy metal" frequently also carries the connotations of pollution and/or toxicity. Table 1 categorizes metallic elements according to biological function and abundance and shows elemental abundances for seawater and the crust of the earth. Not all the elements listed in Table 1 as "essential" are required by every animal and plant—only a few higher plants may require aluminum or vanadium, silicon is an essential bulk component of diatoms not required by other forms, and molybdenum appears to be essential only to organisms that derive their nitrogen by nitrate reduction or fixation of free nitrogen (Underwood, 1962; Epstein, 1965). Similarly, the designation of toxicity is arbitrary, since most of the essential elements are toxic at unusually high concentrations. The nonessential elements include a few (cesium, rubidium, strontium) which consistently occur in organisms and can replace to a large degree the biological functions of essential elements (Rb and Cs for K, Sr for Ca). To a much lesser extent, the metals Cr, Ni, and Cd may fulfill the biological functions of Zn, Mn, or Cu. It should be noted that the metals which are essential or relatively nontoxic to biological systems generally have a low atomic number (only Rb, Sr, Mo, and Cs exceed 30) and are relatively abundant in the biosphere. The toxic metals generally have high atomic numbers (an outstanding exception is Be with an atomic number of 5) and low abundances (notable exceptions include As, Ba, and Pb, all of which occur consistently in living organisms, and Be and Th, which are extremely variable in their biological distribution).

In addition to the elements in Table 1, certain other metals are of concern because of radiation from radioisotopes, whether naturally occurring or introduced from man's nuclear activities. The abundances and composition of radionuclides in the marine environment are summarized elsewhere (Rice and Wolfe, 1971; Joseph et al., 1971). Most of the significant radionuclides are isotopes of certain elements in Table 1 such as chromium, iron, manganese, zinc, cesium, and strontium. To this list we should add cerium,

TABLE 1.—Metallic elements of biological significance.

	Seawater abundance[1]	Crust abundance[2]
	mg/liter	*ppm*
"Essential bulk" elements		
Calcium	400	36,300
Magnesium	1,350	20,900
Potassium	380	25,900
Sodium	10,500	28,300
"Essential trace" elements		
Cobalt	0.0005	23
Copper	0.003	45
Iron	0.01	50,000
Manganese	0.002	1,000
Zinc	0.01	65
Aluminum	0.01	81,300
Molybdenum	0.01	1
Silicon	3	277,200
Vanadium	0.002	110
"Nonessential trace" elements		
Cesium	0.0005	1
Chromium	0.00005	200
Nickel	0.002	80
Rubidium	0.12	120
Strontium	8	450
Tin	0.003	3
"Toxic" elements		
Antimony	0.0005	0.2
Arsenic	0.003	2
Barium	0.03	400
Beryllium	0.0000006	2
Bismuth	0.00002	0.2
Cadmium	0.00011	0.2
Lead	0.00003	15
Mercury	0.00003	0.5
Selenium	0.004	0.09
Silver	0.0003	0.1
Thorium	0.00005	10

[1] Goldberg, 1963.
[2] Mason, 1958.

zirconium, niobium, ruthenium, scandium, and plutonium—all of which occur in only trace amounts in the biosphere, but have radioisotopes which are produced in significant quantities by man and accumulated by animals and plants. In the following discussions "metallic elements" will be used to refer generally to all of the elements mentioned above and in Table 1. Space will not permit separate discussion of each element; instead we will attempt to discuss those general aspects of ecosystem structure and function likely to be most significant in governing the flux of elements within and through estuaries and to identify those elements known to be valid examples or exceptions.

Although an estuarine ecosystem is very complex and difficult to model mathematically, we will take the approach of defining the variables which should be considered in a mathematical model of the dynamic cycling of metals in estuaries, with particular emphasis on the coastal plain estuaries of the southeastern United States.

MAJOR RESERVOIRS IN THE CYCLING OF ELEMENTS

In marine and estuarine environments, nearly all of any given metallic element occurs in the sediments and water (Duke, Willis, and Price, 1966; Duke et al., 1969; Pomeroy et al., 1969; Lowman, Rice, and Richards, 1971). Both sediment and water contain several individual reservoirs for elements, with some components much more important than others to cycling in the system. The "water components" include dissolved ionic forms, dissolved organic complexes, and suspended particulate matter—all of which interact with sediment compartments via adsorption, ion-exchange or sedimentation-resuspension processes. In tracer studies with ^{65}Zn, the rapid instantaneous uptake of radioisotope by estuarine sediments indicated a high rate of continuous exchange of zinc across the sediment-water interface (Duke, Willis, and Wolfe, 1968). In sedimentary deposits, elements may become "trapped" in deeper sediments and be effectively removed from further exchange with the system. In salt marsh, however, *Spartina* recycles phosphorus and zinc from deep subsurface sediments (Pomeroy et al., 1969), and burrowing animals such as crabs, polychaetes, and clams rework shallow and surface deposits, thereby prolonging contact with overlying waters (Gordon, 1966; Rhoads, 1967; Rhoads and Young, 1971). In preliminary studies on the exchange of zinc between estuarine sediments and water, the resuspension of sediments by the burrowing and feeding activity of polychaetes markedly increased the rate of loss of tracer ^{65}Zn from the water overlying the experimental cores (Duke et al., 1968, and unpublished observations). Surface silt layers of high organic content may be a major source of elements to deposit feeders in detritus-based food webs (Cross, Duke, and Willis, 1970; Lowman et al., 1966). In turbulent estuaries, these surface deposits may become suspended and be ingested by filter-feeding organisms such as menhaden, bivalve molluscs, and

zooplankton. Suspended particulate matter may arise also from the ultimate flocculation and precipitation of dissolved ionic species, such as Fe and Al, which are readily hydrated to form colloidal hydroxides at the pH of seawater (Riley and Chester, 1971). Other sources of suspended particulate matter include feces excreted directly into the water column by pelagic animals, cast-off exuviae from zooplankton, and dead planktonic organisms.

Different dissolved chemical species in the water undoubtedly represent discrete and significant reservoirs in the cycling of elements. Organic metallic complexes or chelates may equilibrate slowly with the ionic forms and have been shown or suggested to have drastically different availabilities to organisms. For example, EDTA (ethylenediaminetetraacetic acid) reduced the accumulation of ^{59}Fe by crabs (*Panopeus*), clams (*Mercenaria*), and oysters (*Crassostrea*) (Rice, 1965). Goldberg (1952) demonstrated that the marine diatom *Asterionella japonica* also could utilize iron if particulate or colloidal but not when complexed with citrate, ascorbate, or artificial humate. On the other hand, accumulation of cobalamin by clams (*Donax*) was much enhanced over accumulation of ionic cobalt (Lowman and Ting, in press); and it has been suggested that natural organic chelators may enhance the growth of phytoplankton (Barber and Ryther, 1969), thereby implying that organic complexes might constitute an important avenue for accumulation of metallic nutrients by marine organisms. Unfortunately, technology for the separation and identification of organic ligand-metal complexes from natural waters is in its early infancy, and one can only speculate on the significance of the various chemical forms present in estuarine waters. Regardless of the relative biological availabilities of metals from different organic complexes or from uncomplexed forms, the formation of soluble organic-metal complexes increases the holding capacity of estuarine water for a particular metallic element. Soluble organic complexes therefore probably decrease the net adsorption of metals onto sedimenting particulate materials, thereby increasing the metals' susceptibility to export via tidal flushing. The nonliving elemental reservoirs designated in Table 2 are thought to be of greatest significance in determining the distribution and flux of metallic elements in estuaries.

The estuarine biota consists of many species in a complex and interwoven network of feeding relationships. From a practical viewpoint, all species cannot be considered major elemental reservoirs for modeling purposes. One approach would be to group species by trophic position and consider each trophic level as a single reservoir. Many species, however, are opportunistic feeders with omnivorous habits which complicates their ready assignment to a particular trophic level and necessitates the use of fractional trophic levels. In addition, some species of comparable trophic position and abundances must be considered separately because one is desired as human food and another not. For example, oysters, clams, and scallops should be considered separately from other filter-feeding bivalve molluscs. Another example might be the primary carnivores, flounders and skates, of which only the flounder is harvested for human food. It is more feasible to group species wherever possible and consider individual species only where necessary. Preliminary surveys of the estuarine flora and fauna in the vicinity of Beaufort, N.C., suggest that the organisms in Table 2 should be considered as separate reservoirs or components. Some of the species are identified because of their commercial importance; others only because of their abundance and probable significance as forage. Organisms not identified to species have been lumped arbitrarily into "other" categories according to their feeding habits and trophic position.

The reservoirs identified in Table 2 as being "significant" or "important" in the cycling of elements in estuaries obviously are not all of equal importance. The list is probably incomplete, but at the same time may include some unnecessary designations. Most of the reservoirs identified to species have been considered in the development of a static model of annual energy flow in these estuaries (Williams and

Murdoch, 1970).[2] Quantification of the biomass in each of the major biological components is a primary objective of ecological research at the Atlantic Estuarine Fisheries Center, and preliminary estimates are currently available for the dominant macroorganisms (Williams, Thayer, Price, Kjelson, and Turner, Unpublished data). Analytical data on the concentrations of iron, manganese, zinc, and copper in these organisms and in sediments and water are also available or forthcoming (Cross et al., 1970; Cross and Brooks, in press; Wolfe, 1970a; Cross, Lewis, and Hardy[3]). Meaningful quantification of reservoir size for any element in certain components, however, will be extremely difficult to achieve (especially for the "other" categories, e.g., filter-feeding bivalves, deposit-feeding bivalves, carnivorous benthos, etc.). It may be practical to evaluate the importance of these "catch-all reservoirs" only by manipulating trial values for biomass and elemental concentrations during early phases of model development.

Pathways of elemental flux between reservoirs also are tentatively identified in Table 2. Individual transfer processes are designated in the matrix of Table 2 by an "I", indicating an influx of a metallic element from the reservoir at the top of the table to the reservoir on the left. Fluxes between biological reservoirs represent food chain transfers of elements. Such transfers usually involve one-way cyclic net flows (with internal loops) through the food web of the ecosystem. At this time the feeding habits of many of the listed species are incompletely known, and the food web of Table 2 must be regarded partly as the product of intuition and speculation.

The flux of elements between the organisms and the nonliving reservoirs is less readily identified, however, than the food web, because of uncertainty about the relative abundance and importance of different physical-chemical states, e.g., the ionic forms versus organic complexes. Physical-adsorption and ion-exchange processes, operative on biological (and nonbiological) surfaces, obviously would contribute to the total flux of an element; but since these processes are generally reversible, their importance to net transfers (especially at higher trophic levels) remains unknown. There must be a net influx of most elements from the soluble ionic phase to most organisms during their life span, however, simply because the surface area for adsorption increases during growth.

The significance of organic-metal complexes is unknown. We suspect that dissolved organic compounds constitute a mechanism for internal feedback loops involving all organisms at all trophic levels, except perhaps man. Thus, an organism may accumulate specific organic-metal complexes which undergo metabolic transformation, and the metals may in part be excreted as different organic complexes which reenter the cycle as nutrients for phytoplankton or heterotrophic microbes. We can only speculate now on whether there is net production or net utilization of metal-organic complexes by organisms. This ambiguity is indicated in Table 2 by a "double I" (i.e., by I's at both relevant intersects of the matrix), representing ingestion or absorption of organic-metal complexes by most organisms with simultaneous excretion of other organic complexes which might be quite different chemically.

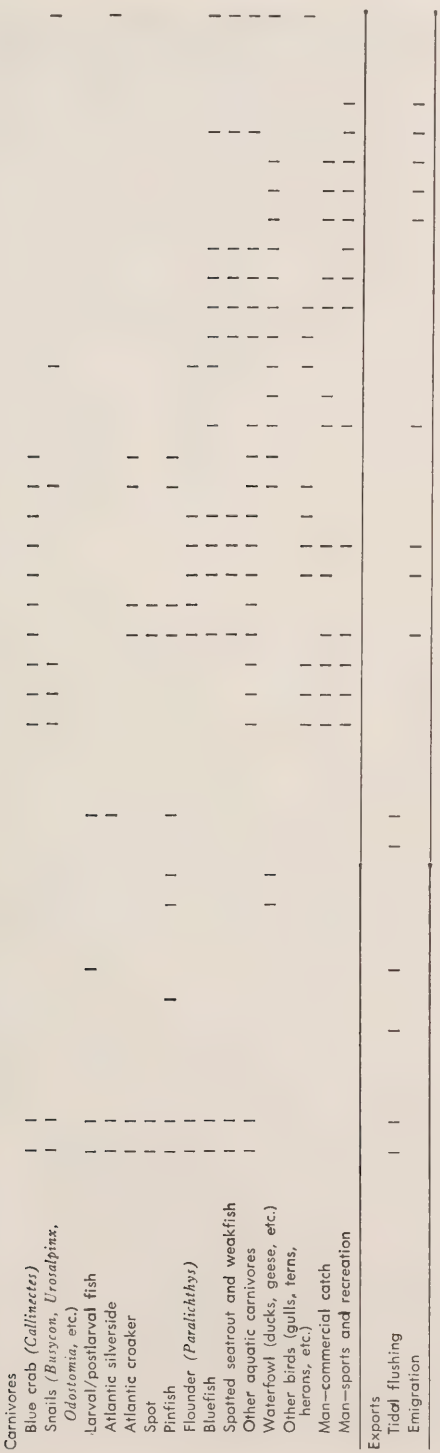
Fluxes between nonliving reservoirs are more dependent upon reversible physical processes, such as adsorption, ion-exchange, and sedimentation-resuspension. The net direction of flux may therefore depend on such variables as salinity, pH, and turbulence. The association of heterotrophic microbes with suspended particulate material probably results in a net influx of most metals into this reservoir from soluble sources with subsequent passage into detritus-based food chains. The extent of reversibility for the transfers (identified by "R" in Table 2) varies also from element to element. Thus, ^{137}Cs may be transported into estuaries on bed-load sediment and desorbed at higher salinities

[2] Williams, R. B., and M. B. Murdoch. 1970. A general evaluation of fishery production and trophic structure in estuaries near Beaufort, N.C. *In* Center for Estuarine and Menhaden Research Annual Report to the Atomic Energy Commission. Filed at NMFS Atlantic Estuarine Fisheries Center, Beaufort, N.C. 28516. [Processed.]

[3] Cross, F. A., J. M. Lewis, and L. H. Hardy. Concentrations of Mn, Fe, Cu, and Zn in four species of filter-feeding bivalve molluscs. Unpublished manuscript filed at NMFS Atlantic Estuarine Fisheries Center, Beaufort, N.C. 28516.

TABLE 2.—Major reservoirs and pathways of elemental flux in an estuarine ecosystem.
I = influx from top to left; R = reversibility (see text)

	Soluble ionic	Soluble organic	Interstitial soluble	Subsurface sediments	Bed-load sediment	Surface sediment deposits and microflora	Suspended particulate detritus and microflora	Salt grass	Benthic algae and epiphytes	Eelgrass and epiphytes	Phytoplankton	Zooplankton	Heterotrophic microbes	Meiofauna	American oyster	Hard clam	Bay scallop	Shrimp (*Penaeus*)	Shrimp (*Palaemonetes*)	Atlantic menhaden	Striped mullet	Bay anchovy	Other filter feeders	Other deposit feeders	Blue crabs	Snails	Larval/postlarval fish	Atlantic silverside	Atlantic croaker	Spot	Pinfish	Flounder	Bluefish	Spotted seatrout and weakfish	Other carnivores	Water fowl	Other birds	Import from watershed or precipitation or human effluents	Import via immigration
Nonliving reservoirs																																						
Soluble ionic													I																								I	
Soluble organic	R					I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	
Interstitial soluble	R	R																																			
Subsurface sediments			R			I																															
Bed-load sediment	R		R																																	I	
Surface sediment, detrital deposits and microflora	R	R	R		I			I	I	I					I	I	I						I		I	I											
Suspended particulate, detritus and microflora	R	R			R	R		I	I	I	I	I								I	I	I					I	I	I	I	I	I	I	I	I	I	
Primary producers																																					
Salt grass (*Spartina*)	I	I	I																																		
Benthic algae and epiphytes	I	I																																			
Eelgrass and epiphytes	I	I		I		I																															
Phytoplankton	I	I																																			
Herbivores																																					
Zooplankton	I	I					I				I																										
Heterotrophic microbes	I	I				I	I	I	I	I				I	I	I	I																				
Meiofauna	I	I	I			I																															
American oyster (*Crassostrea*)	I	I					I				I																										
Hard clam (*Mercenaria*)	I	I					I				I																										
Bay scallop (*Argopecten*)	I	I					I				I																										
Shrimp (*Penaeus*)	I	I				I					I																									I	
Shrimp (*Palaemonetes*)	I	I				I																															
Atlantic menhaden	I	I					I				I	I																								I	
Striped mullet	I	I				I	I				I	I		I																						I	
Bay anchovy	I	I					I				I	I																									
Other filter feeders	I	I	I				I				I																										
Other deposit feeders	I	I	I			I			I	I				I																							



(Wolfe, 1971); whereas ^{65}Zn may be irreversibly adsorbed onto estuarine sediments (Johnson, Cutshall, and Osterberg, 1967). The actual flux of any given element through the complex interwoven network of pathways tentatively identified in Table 2 is in a state of dynamic equilibrium affected by system imports and exports and by a number of environmental variables, to be discussed in the following sections.

INPUTS AND OUTPUTS OF ELEMENTS TO AND FROM ESTUARIES

System inputs and outputs consist of the physical translocation of elemental reservoirs (sediment, water, and biotic components) across the boundaries of the estuarine system (Table 2), and fluxes of other materials (nonreservoirs) which influence the distribution or movement of elements among the system reservoirs. Rainfall is a dominating system input, which introduces small amounts of some elements directly as aerosols (Gorham, 1961), but exerts its greatest influence in the form of runoff. The volume and flow rate of runoff in turn determine the amount and composition of elements leached from the land and the size of the bed load of eroded sediment transported into the estuary. The volume and flow of runoff also interact with the tidal volume to affect the flushing rate for the estuary. Tidal flushing continuously removes from the estuary a fraction of the dissolved and suspended materials, including the planktonic reservoirs. The tidal volume also represents an input of ocean water, but since seawater contains less of most metallic elements than estuarine waters, net loss from the estuary probably results. If, on the other hand, the coastal or estuarine waters contained an excess of uncomplexed organic material, seawater might represent an input of soluble ionic metallic elements which could accumulate in the estuary through sedimentation, or be removed from the estuary as organic complexes, either by flushing or bioaccumulation.

Variable wind speed and direction affect water circulation patterns particularly in shallow estuaries and thereby vary the "normal" flushing characteristics of an estuary. Circulation within

the estuary obviously determines also the physical distribution of certain reservoirs within the system, and this aspect of cycling compounds the difficulties of developing a realistic model. Application of the term "ecosystem" to an estuary, however, implies that an estuary behaves as a discrete, identifiable unit and, despite the clumped distributional patterns exhibited by organisms in the environment, spatial distribution of reservoirs within the system is assumed insignificant; i.e., the system model is homogeneous.

In addition to tidal flushing of planktonic organisms, biotic inputs and outputs include the contribution of terrestrial primary productivity, brought into estuaries as dissolved organic material and particulate organic detritus in runoff, and the seasonal migrations of larger invertebrates and fish into and from estuarine waters.

A final input which must be considered consists of human waste materials. Organic waste materials affect productivity and biological species structure of the ecosystem and probably also affect the availability of metallic elements through organic complexing. In addition, large amounts of certain metallic elements are introduced into many estuaries directly in industrial and municipal effluents.

FACTORS INFLUENCING DISTRIBUTIONS AND TRANSFERS OF ELEMENTS AMONG THE VARIOUS RESERVOIRS IN ESTUARIES

The various groups of biota, the dissolved and particulate components in the water column, and sediment compartments, represent the major reservoirs per se for metallic elements, but the interaction of these compartments and regulation of their sizes are influenced greatly by other variable characteristics or components of estuarine ecosystems including inputs of energy and auxiliary materials or factors which affect reservoir sizes or transfer rates within the system. These factors represent "nondynamic state variables" in the modeling terminology of Kowal (1971). These characteristics may be categorized as: (1) those that affect productivity in the trophic web and (2) those that affect the physical state or rates of exchange between components for the specific elements of interest. The influences of major nondynamic state variables are summarized briefly in Table 3.

Solar energy is perhaps the best example of the first type of input. Solar energy drives the primary productivity supporting all the biotic reservoirs and establishes the basic temperature regime for the entire system, which is a dominant factor influencing the rate of material transfer processes, biological and nonbiological. The seasonal variability of temperature can readily be incorporated into systems models according to a sinusoidal function. This general approach has been described and applied by Williams (1969). In the first category also are dissolved gases, e.g., CO_2 and O_2, and inorganic nutrients, especially the various forms of P and N. Certain dissolved organics may also be included here, although absolute requirements for these have not been demonstrated in the nutrition of estuarine organisms, and dissolved organic-metal complexes constitute a major reservoir already considered. Acidity, or pH, is an important factor in that it acts with temperature to control CO_2 solubility and thereby affects primary productivity, but pH also falls into the second category because it determines the equilibrium distribution of metals in adsorption reactions, i.e., exchange between water and sediments, or between water and biological surfaces; and in chelation reactions, including metal-organic complexes in the dissolved phase.

Wind is another significant energy input in shallow estuaries. Wind increases turbulence and suspension of particulate matter which promotes exchange of elements between water and sediments and affects the size of the suspended particulate reservoir subject to flushing.

Salinity is also a determinant in the distribution and cycling of elements. Salinity, as a measure of ionic strength, affects the adsorption equilibria established between sediments and water and biological surfaces and water, and probably also influences the configuration of proteins and other biological polymers which form complexes with metals. This mechanism may be the basis of salinity effects on active transport processes in ionic and osmotic regulation in es-

TABLE 3.—Role of nondynamic state variables.

Factor	Compartment and sign (+ or −) of correlation	
Fe, Al, Mn, etc.	Suspended particulate	+
Nutrients (nitrate, nitrite, ammonia, phosphate, and silicate)	All primary producers and microbial heterotrophs	+
Solar insolation	All primary producers	+
Temperature	Exchange rates	+
	Adsorption	−
	Respiration	+
Season of year	Inputs and outputs via migrations	±
Wind speed and wind direction	Suspended particulate	+
	Flushing export rate	±
Dissolved carbon dioxide	All primary producers	+
Dissolved oxygen	Respiration	+
pH	Surface adsorption	+
Salinity	Surface adsorption	−
	Ion-exchange rates	+
Precipitation	Inputs of sediment bed-load	+
	Suspended particulate	+
	Dissolved ionic	+
	Dissolved organic	+

tuarine organisms. In addition, salinity provides a measure of bulk components of seawater, e.g., Ca and K, which may compete directly with trace components for adsorption sites of biological accumulation, e.g., Sr and Cs. For example, increasing salinity decreases the accumulation rate and concentration factor for ^{137}Cs in estuarine clams (Wolfe and Coburn, 1970). Salinity is correlated also with the concentration of ^{137}Cs in lower-salinity estuarine water, possibly as a result of mass action on the sediment-water exchange equilibrium (Wolfe, 1971). Important dissolved trace components include Fe, Al, and Mn, whose concentrations depend less on salinity than on watershed characteristics and runoff. At the pH, Eh, and ionic strength characteristic of seawater, these elements form insoluble hydroxides which flocculate and provide adsorptive surfaces for other elements. Such a coprecipitation process may be an important determinant in the distribution of fallout ^{106}Ru in estuaries (Wolfe and Jennings, in press).

For any given estuary the chemical environment and flushing characteristics are affected greatly by the geological and chemical characteristics of the watershed area, the type of estuary (stratified vs. well-mixed, etc.), and the physical size, shape, and orientation of the estuarine basin. Such characteristics must be considered when different estuaries are compared.

A set of biological processes accompanies each trophic interaction and determines the efficiencies for transfers of biomass between components. These are feeding or ingestion rate, digestion rate, assimilation efficiency, respiration, and growth efficiency. Each of these characteristics may be influenced in turn by various environmental factors, such as temperature and salinity (Peters and Boyd, in press; Peters and Angelovic, in press).

Assimilation and respiration maintain the biomass of the biological reservoirs for elements, but the accumulation and retention of most metallic elements are probably not directly correlated with the assimilation and respiration of carbon. For dynamic modeling of the cycling of metallic elements in the estuarine biota, however, it is essential to consider the changes in biomass as well as changes in concentration of the element of interest. The interrelation of ^{65}Zn-excretion and respiration has been examined directly for pinfish, *Lagodon rhomboides*, (Hoss, 1971). Lowman et al. (1971) computed assimilation efficiencies ("conversion factors") for the transfer of several metallic elements from oceanic phytoplankton to zooplankton, based upon

relative concentration factors in zoo- and phytoplankton and a mean carbon assimilation of 50%. On this basis, assimilations for 24 elements ranged from 1 to 85%—indicating nonparallelism with carbon assimilation—but Lowman went on to say: "The major weakness in this method of calculating conversion factors for a variety of elements is the uncertainty of the accuracy of the concentration factors for phytoplankton and zooplankton." Similar uncertainty exists for published concentration factors for various elements in estuarine organisms, especially since environmental conditions (and therefore elemental concentrations in estuarine water) are subject to such wide variation. A further complication is the uncertainty concerning the proportion of total elemental intake represented by food sources. According to Polikarpov (1966), marine animals satisfy their requirements for most elements by direct absorption from the surrounding water. Considerable experimental evidence, however, supports the importance of food as a source of elements for many organisms (Rice, 1963; Hoss, 1964; Baptist and Lewis, 1969). Atoms adsorbed directly from the water onto body surfaces, whether internal or external, do contribute to the concentration factor but have no relevance to assimilation of food. Surface adsorption frequently results in assimilation, however, as in phytoplankton (Goldberg, 1952) and the mantle epithelium of Pelecypoda (Nakahara and Bevelander, 1967). For organisms with well-defined and easily analyzed internal tissues, e.g., crustacean and fish muscle, internal concentrations of elements probably represent the assimilated fraction, but for many smaller or less differentiated organisms, internal tissues cannot readily be separated from adsorptive surfaces. Assimilation efficiency may depend also on biochemical composition of the food —at least at certain trophic levels. For example, the assimilation of ^{65}Zn by human subjects was 35% from a diet of whitefish (Honstead and Brady, 1967) and 13.5% from oysters (Honstead and Hildebrandt, 1967), showing a high (though perhaps coincidental) positive correlation with the protein content of the foodstuff (Wolfe and Rice, 1968).

The concentration of an element in representatives of a population of organisms is a function of the turnover time for the element and the average life span of the organism. Long-lived organisms probably achieve a steady state for the turnover of most elements after the cessation of growth—and if the availability of the element from the organism's environment is stable. In organisms with rapid growth and high population turnover, net accumulation probably proceeds for most metallic elements throughout the entire short life span of the organism, and steady state is not reached before the organism is consumed by the next trophic level. The environmental and physiological factors determining the steady state conditions are not known, however. Many organisms may accumulate metallic elements far in excess of their biological requirements (Wolfe, 1970b; Pequegnat, Fowler, and Small, 1969), and accumulation of metals may continue independent of the biological necessity in some cases until available reaction sites (e.g., between metal and proteins or tissue surfaces) are saturated. This process is suggested also by the increasing concentration of mercury with age (or size) in various fish (Westöö, 1969; Bache, Gutenmann, and Lisk, 1971).

In a dynamic estuarine system, where environmental levels of metallic elements are subject to rapid fluctuations, the organismic response to environmental change must be identified. Information of this nature is sorely lacking in the literature. Pringle et al. (1968) tested the response of oysters to various increased experimental levels of lead, and after 49 days exposure, accumulation had proceeded in direct relation to availability of lead in the environment. Other data (Chipman, Rice, and Price, 1958; Preston, 1967; Wolfe, 1970a) suggest that concentration factors for Zn in oysters are inversely related to zinc content of water, implying that net accumulation would diminish or cease at some high environmental concentration (low concentration factor in oyster) and steady state would be established. In these cases, however, the variability of instantaneous uptake of the element can only be inferred from the amounts contained after a long period of accumulation. In natural ecosystems, fallout radioisotopes appear in estuarine organisms very quickly after initial entry of the

isotopes into the ecosystem (Wolfe and Schelske, 1969; Wolfe and Jennings, in press). A high rate of instantaneous uptake has also been demonstrated for many organisms and many elements in experiments on radioisotope accumulation, but, in most cases, concentrations of stable element counterparts for the radioisotopes were undetermined so that rates of flux for the stable element could not be computed from the observed flux of radioactivity. Although the accumulation and turnover of a radioisotope in a single component can be modeled mathematically independent of the stable element chemistry (Reichle, Dunaway, and Nelson, 1970), it is the flux of stable elements which determines the movement of radionuclides among the various components of an ecosystem and investigators should routinely collect data on the stable element composition of the compartments involved in their accumulation studies. In this way, experimentally observed radioisotopic accumulation rates can be used in conjunction with the specific activity, i.e., the concentration ratio of radioisotope to total element, to determine rates of elemental turnover. It seems probable that instantaneous uptake of an element is a direct function of available environmental levels whereas instantaneous loss is a direct function of accumulated amounts. The instantaneous uptake rate is also a function of other environmental variables. For example, in the estuarine clam *Rangia cuneata*, the instantaneous uptake rate and the equilibrium concentration of ^{137}Cs increase with temperature and decrease with salinity (Wolfe and Coburn, 1970). Salinity, temperature, pH, and total Zn also influenced the accumulation of ^{65}Zn by various estuarine organisms under experimental conditions (Duke et al., 1969).

Net accumulation (or net loss) results when instantaneous uptake exceeds (or is less than) instantaneous loss, and the physiology and metabolism of the organism determine the residence times required for passage through its many alternate internal compartments and pathways. Retention times are usually discussed in terms of biological half-life. (See for example Baptist, Hoss, and Lewis, 1970.) Since organisms have several compartments simultaneously interacting with the environment, retention typically consists of several components with different rates. One might expect the faster rates to be associated with surface adsorption reactions, intermediate rates with excretion of unassimilated material as feces, and slow rates with the turnover of the assimilated and metabolized fraction of the elemental content. Although the relative amounts of an accumulated radioisotope involved with different retention components can be determined for the particular conditions and time period of accumulation and loss used in the experiment, these amounts will not be representative of stable element pools unless all of the internal compartments are equally labeled, i.e., to a uniform specific activity. Thus, long-term accumulation experiments under conditions of constant specific activity are required (Cross, Willis, and Baptist, 1971). The individual retention components for an element probably will have to be considered for each important reservoir in modeling the overall flux of that element in the ecosystem.

We have discussed several aspects of elemental cycling in estuaries and have demonstrated the incompleteness of man's knowledge of how an estuary operates as a system with many integral, smoothly functioning components. We believe, however, that many of the unsolved problems which have presented themselves will be realistically resolved only by a holistic approach to ecological research. The foregoing discussion represents an effort to conceptualize the elemental cycling system that operates in our southeastern coastal zone estuaries. Prior recognition of the complexity and integrity of the system as a whole provides an improved basis for planning meaningful research on the transfer processes between individual components of an estuary. Considerable research is required before we can actually quantify the reservoirs, routes, and rates of elemental flux involved in this preliminary model of these ecosystems. The complexity of the ecosystem defies precise quantification of all the reservoirs and all the transfer rates under any set of environmental conditions. In such a system, however, the predictability of the magnitude and variability of any elemental reservoir depends upon recognition of all the interactions impinging upon that reservoir. Research now

in progress at the Atlantic Estuarine Fisheries Center will enable us to estimate the size ranges for most reservoirs of manganese, iron, and zinc in our local estuarine system. The major gaps in our present knowledge lie in:

1. Determining the relative amounts of different physico-chemical forms of an element or radioisotope in natural waters, their relative stabilities, and the ease of interconversion between the various forms.

2. Determining the relative biological availabilities of these different physico-chemical forms to various types of biota.

3. Determining trophic structure of the entire ecosystem. The role of microorganisms—as sources of metallic elements to consumers in detritus-based food chains, as producers of organic-metal complexes, and as remineralizers of metals previously incorporated into plant or animal tissues—is particularly poorly understood.

4. Determining feeding rates and assimilation efficiencies for carbon and metallic elements at each major trophic interaction.

5. Determining biological retention of metallic elements in the major organisms consumed by man.

6. Determining the interactions of variable environmental parameters on reservoir size and transfer rates at each step in the overall system.

As further information becomes available, this preliminary systems model will be refined and tested as to its adequacy for describing the flux of manganese, iron, and zinc in our local estuarine system. Maintenance of this sort of holistic viewpoint toward ecological function and continuous updating of existing conceptual models will provide the most reliable basis for rational management of man's releases of toxic heavy metals and radionuclides—or indeed, of any contaminant additions to the environment.

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A LABORATORY STUDY OF PARTICULATE AND FILTER FEEDING OF THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

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ABSTRACT

In laboratory feeding trials Pacific mackerel, *Scomber japonicus*, averaging 147 g in weight did not respond to *Artemia* nauplii, but did capture *Artemia* adults by biting (particulate feeding) when density was 1 or 2/liter and by filtering when density was 22 to 112/liter. Particulate feeding is described by $N_P = 60.3tD$, where N is the number of *Artemia* ingested in t minutes at D numbers per liter. Filter feeding is described by $N_F = 23{,}788\ (1 - e^{-0.0036tvD})$, where 23,788 is an asymptotic estimate of the number of *Artemia* in the digestive tract at full capacity.

The results suggest that the mackerel utilizes only the larger of the planktonic crustaceans, such as euphausiids, in the sea. For the relatively low average densities of such organisms the derived equations indicate that the mackerel could not obtain its daily nutritional requirement, estimated to be 8% of body weight, in less than 24 hr of feeding. Though the daily requirement could be obtained in much shorter periods, perhaps by filter feeding, if such crustaceans are encountered in aggregations of considerably higher density than reflected by area averages, it is probable that the mackerel must often depend in part on such larger organisms as fish to fulfill its needs.

Comparison of the mackerel ingestion rates to those for the smaller northern anchovy indicates that while the individual mackerel may generally capture a greater proportion of the large crustaceans encountered than the anchovy, the proportion captured would have a relatively lower nutritional value for the mackerel.

The Pacific mackerel, *Scomber japonicus*, is one of several pelagic schooling fishes of the eastern temperate Pacific which feed on zooplankton, but it does not depend entirely on zooplankton. Fitch (1956) reported that stomach contents contained about 30% larval and juvenile fish by volume, with the remainder composed largely of such crustaceans as mysids, copepods, and euphausiids. Frey (1971) commented that larval and juvenile fish appear to be the most important food, but that the mackerel relies heavily on euphausiids at times. Hatanaka et al. (1957) showed that *S. japonicus* in coastal regions of Japan consume mainly small anchovies in the late summer and autumn and euphausiids in other seasons. The biomass of euphausiids consumed annually was estimated to be three or four times that of anchovies.

In addition to being the dominant element in the diet of *S. japonicus*, the larger crustaceans are an important class of food for a number of other pelagic schooling fishes. The jack mackerel (*Trachurus symmetricus*) is known to feed heavily on small fish and squid at times (Fitch, 1965), but about 70% of stomach contents by volume is euphausiids (Carlisle, 1971). The Pacific sardine (*Sardinops caerulea*) feeds largely on copepods smaller than those consumed by the jack mackerel but is occasionally gorged on euphausiids, and these average about 5% of stomach contents by volume (Carlisle, 1971). The northern anchovy (*Engraulis mordax*) consumes phytoplankters and small zooplankters, but large copepods and euphausiids appear to be the most important food items (Loukashkin, 1970). Thus while all of these species prey on

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large crustaceans, the latter do not necessarily make an equivalent contribution to their diets. It is probable that the segment of the biota represented by such crustaceans in the sea is a food source of different potential for different fishes.

Assessing the food potential of large crustaceans for the Pacific mackerel, or any of the above teleosts, requires a knowledge of the density levels of such crustaceans in the sea and of the rates at which the organisms can be captured in relation to density. Leong and O'Connell (1969) determined by a laboratory study the rates at which the northern anchovy feeds on *Artemia* nauplii by filtering and on *Artemia* adults by biting (particulate feeding), and O'Connell (1972) showed that the two kinds of feeding activity in a small school varied with the relative abundance of the two sizes of *Artemia*. The present study was undertaken to obtain comparable information for the Pacific mackerel, using *Artemia* as the food. The results are discussed in respect to the densities of large crustaceans in the sea and in respect to the feeding rates of the anchovy.

METHODS

Feeding trials were carried out in an arrangement of two plastic pools with a connecting trough and gates (Leong and O'Connell, 1969; O'Connell, 1972). The pools were supplied with a continuous flow of filtered sea water and each contained 4.5 m^3 of water at a depth of 0.61 m (2 ft). They were under a 12-hr day, 12-hr night cycle of illumination, but all trials were carried out during the day. Temperature varied from 16° to 19°C.

A school of about 160 mackerel was acclimatized in the pool arrangement with the gates open for about 2 weeks and then confined to one pool before the study started. The fish averaged 222 mm (202 to 247 mm) in standard length and 152 g (100 to 225 g) in weight. The latter average is based on weights taken at the end of each feeding trial and included digestive tract contents, which were later found to range from 0.1 to 21.8 g. These values were subtracted from the measured fish weights to obtain estimates of the weights before feeding. The subsequent analysis involves the adjusted weights, which averaged 147.3 g.

All feeding trials were preceded by at least 24 hr without feeding, which was enough to produce virtually empty digestive tracts in preliminary investigations. For each trial the water flow was turned off, and four fish were diverted from the holding pool to the trough and then admitted to the prepared food situation in the other pool where they were allowed to feed for a given number of minutes. Closing of the gate after admission initiated the time period and introduction of a hinged crowder, which was rapidly closed to trap and remove the fish, terminated the time period. The fish were killed in less than 2 min after introduction of the crowder, immediately measured and weighed, then placed in jars of 10% Formalin with the body cavity opened.

Though the study is concerned primarily with feeding on *Artemia* adults, a few feeding trials were carried out with newly hatched *Artemia* nauplii, which averaged 0.65 mm in length, to document the response of the mackerel to very small crustaceans. The densities in the water were estimated from subsamples, and quantities in the digestive tracts were estimated by total counts or volumetric aliquoting, as described by Leong and O'Connell (1969).

Feeding on *Artemia* adults is based on digestive tract contents of four fish in each of 28 trials, with each trial representing a different combination of food density and feeding time (Table 1). The food situation was established for each trial by placing a given wet weight of *Artemia* adults in the experimental pool and dispersing it gently with wide-mesh dip nets just before admitting the fish. The weights given under food quantity are the wet weights introduced at the start of each trial. These were selected after preliminary observation to include the highest and the lowest levels that could be managed conveniently. The multiplication factors given in certain cells of the table indicate the number of times the specified weight was introduced into the pool during the trial, e.g., 20 g was introduced six times, or at 15-min intervals, during the 90-min trial. This was done to sustain the nominal food den-

TABLE 1.—The array of trials with respect to food density and feeding duration. Number/liter is the nominal density for the weight introduced.

Quantity of *Artemia*		Minutes of feeding					
Total weight	Number liter	2.5	5	10	30	60	90
g							
10	1	1	1	1	1(3×)[1]	1(6×)	1(9×)
20	2	1	1	1	1(2×)	1(4×)	1(6×)
200	22	1	1	1	1	1	1
590	66	1	1	1	1	1	1
1,010	112	1	1	1	1	--	--

[1] The multiplication factors show the number of times, at equal intervals, that the specified weight was introduced during the trial to maintain the nominal density. See text.

sity over long periods at the lower food density levels. Introduction of food during the trial, and even brief dispersion with the wide-mesh net, did not appear to distress the fish and scarcely interrupted their feeding activity.

The intervals of food introduction for the lower density levels were determined from a preliminary study. During a 30-min trial with 20 g of *Artemia*, e.g., feeding activity declined sharply after 15 min, and average digestive tract contents did not differ from that for a trial of 15 min. A trial of 30 min with two introductions of 20 g showed approximately double the digestive tract contents of the above two. The 10-min interval for 10 g introductions was established from similar considerations. Food availability remained high throughout the trials at the three higher density levels.

The nominal densities of *Artemia* shown in Table 1 are based on the volume of the pool and a conversion factor of 500 *Artemia* adults/g wet weight. The conversion factor is an average derived from samples from the several batches of *Artemia* delivered to the aquarium. Portions of these samples also indicated that individuals averaged 4.5 mm in length and 0.48 mg dry weight.

The quantities of *Artemia* in the digestive tracts of the fish were estimated separately for the mouth, the esophagus and stomach combined, and the anterior and posterior halves of the intestine. The contents of the esophagus and stomach were weighed. Numbers in the various sections were estimated by total count where quantity was low, but by counts from aliquots where the quantity was large. These data indicated that the weight of ingested *Artemia*, determined 2 to 6 months after preservation, was 25 to 50% lower than the weight of the live organisms. Digestion and leaching by Formalin may have been responsible for such loss. Since the weights of food in the digestive tracts could not be considered representative of the weights of food consumed, the analysis was carried out on the numbers of organisms in digestive tracts.

Values for all sections of the digestive tract were pooled to obtain estimates of total digestive tract contents, the primary entity in analysis. The numbers found in the mouth varied from less than 1 to 53% and averaged 18% of total digestive tract contents. This percentage, furthermore, varied with food density, increasing from 4% at the 10 g level to 41% at the 1,010 g level. It is presumed that the contents of the mouth were accumulations to be swallowed and/or material regurgitated during capture. Proportions in the intestine were considerably lower and will be described later.

RESULTS

RESPONSE TO *ARTEMIA* NAUPLII

Three trials were carried out with newly hatched *Artemia* nauplii as the only available food. In two cases the average densities of nauplii were about 190/liter and 230/liter, and groups of four fish showed no recognizable feeding activity during 30-min periods of exposure. In the third case density was a little more than 200/liter and a group of approximately 50 fish showed no feeding activity. The stomachs of five fish from these trials contained no nauplii, although a few nauplii were found on the gill rakers of two of them.

One trial was carried out with *Artemia* adults and nauplii both present in the water. The density of adults was 22/liter and the density of nauplii was 185/liter. After feeding for 5 min, four fish averaged 2,334 *Artemia* adults and 823 *Artemia* nauplii (635 to 1,083) in the mouth, stomach, and esophagus combined. The bulk of both sizes of organism was in the stomachs.

From these results it is evident that while the Pacific mackerel did not respond to nauplii alone,

it did ingest them along with the larger *Artemia* when both were present in the water. However, the dry weight of the nauplii ingested would be about 0.1% of the dry weight of the adults ingested. It appears, also, that the uptake of nauplii was only about 4% as efficient as the uptake of adult *Artemia*, i.e., the number of nauplii per fish represents 4.4 liters of water in the pool, while the number of adults per fish represents 106 liters.

Yasuda (1963) obtained results comparable to the above for *S. japonicus* 120 to 130 mm in length. He found that the mackerel did not eat brine shrimp (0.38 mm in length and presumably nauplii) as did anchovies (*Engraulis japonica*) and even horse mackerel (*Trachurus japonicus*) of approximately the same length. The spacing between gill rakers and gill raker processes was shown to be smaller in the latter two species than in the Pacific mackerel.

RESPONSE TO *ARTEMIA* ADULTS

The 28 trials in which *Artemia* adults were the only available food showed that feeding was particulate at the two lower density levels and filtering at the three higher density levels. Particulate feeding is the capture of individual organisms by directed biting. Filter feeding is the process of straining organisms from the water as it passes through the gill rakers while the mouth remains open. The duration of mouth opening was 1 to 3 sec, and such mouth openings occurred almost rhythmically 15 to 20 times/min. Filtering, however, was sustained for only a limited time, and this time varied inversely with density level of the food. It lasted 30 min at 22 *Artemia*/liter, 20 min at 66 *Artemia*/liter, and about 15 min at 112 *Artemia*/liter. At these times the fish noticeably reduced swimming speed and shifted to particulate feeding. Though particulate feeding appeared to be less vigorous under these circumstances than at the two lowest food densities, complete cessation of feeding did not occur in any of the trials.

The trial groups of four fish evidenced some discomfort upon encountering the highest food density, 112 *Artemia*/liter. Swimming speed and coloration showed less increase than at other densities, and filtering intervals were shorter and less rhythmic. A school of about 70 fish introduced to this highest density, on the other hand, exhibited strong rhythmic filtering accompanied by marked intensification of color and increased swimming speed. Though digestive tract contents from the fish of this group were not significantly greater than for the four-fish group after 5 min of feeding, the larger group virtually eliminated the available food in this time while the smaller group did not noticeably affect its density.

Preliminary analysis indicated that there was no confounding of size of fish with density levels and suggested that the larger fish tended to consume slightly more food at all densities. Hence, estimates of total digestive tract quantities were standardized to the average adjusted weight of all fish (147.3 g) by simple proportion. The means and standard errors of the standardized numbers are shown for each trial in Table 2. The greatest change in a trial average resulting from standardization was 20% of the original estimate, and the change was 5% or less for half of the trials. Standardization also affected the estimates of variability, but only to the extent that the coefficients of variation averaged 1% higher.

A separate analysis for each of the food density levels indicated that digestive tract contents increased proportionately with time at the two lower densities, but increased exponentially toward an asymptotic value at the three higher densities. It was also evident that the density-specific rates of increase varied directly with density for the two lower levels and with the square root of density for the three higher levels. The modes of food accumulation for the two density ranges can therefore be expressed as

$$N_P = \alpha t D \qquad (1)$$

and

$$N_F = N_\infty \left(1 - e^{-\beta t \sqrt{D}}\right) \qquad (2)$$

where N_P = number of organisms in the digestive tract after t minutes of particulate feeding,

TABLE 2.—The average fish weight and the mean ($\bar{X}$) and standard error (SE) of the standardized number of *Artemia* in the digestive tract for each trial.

Density: Number/liter	Feeding duration	Number fish	Average fish weight	Number in digestive tract: $\bar{X}$	SE
	min		*g*		
1	2.5	4	125	149	60
	5	4	130	299	168
	10	4	136	572	86
	30	4	134	2,280	373
	60	3	135	3,430	342
	90	4	150	5,620	216
2	2.5	4	149	254	37
	5	4	148	695	81
	10	3	149	1,530	163
	30	4	123	4,636	583
	60	4	157	5,790	684
	90	4	149	11,325	1,204
22	2.5	2	136	745	263
	5	4	159	2,013	101
	10	3	141	4,399	270
	30	3	135	10,893	790
	60	4	165	15,664	648
	90	4	152	18,079	1,143
66	2.5	3	159	1,502	197
	5	3	139	4,041	409
	10	4	158	5,232	858
	30	4	174	9,863	990
	60	4	158	12,676	484
	90	4	168	15,723	605
112	2.5	3	145	3,079	936
	5	3	155	3,617	447
	10	4	139	7,629	982
	30	4	147	15,845	2,600

N_F = number of organisms in the digestive tract after t minutes of filter feeding,

D = the nominal density of food in numbers per liter,

N_∞ = asymptotic number of organisms in the digestive tract at full capacity,

α = specific feeding rate, and

β = instantaneous feeding rate.

Fitting all of the data in the two low density series with equation (1) and those in the three high density series with equation (2) resulted in a satisfactory fit for the low density group but not for the high density group. Calculated values tended to be lower than trial values for the 22 *Artemia*/liter series, and higher than trial values for the 66 *Artemia*/liter series, particularly for the longer time periods. The difficulty arises from the fact that average quantities in the digestive tracts were lower for the 66 *Artemia*/liter level than for the 22 *Artemia*/liter level in the 30-, 60-, and 90-min trials. The reason for this is not known, but examination of the quantities in the anterior and posterior halves of the intestine for all trials (Table 3) offers a plausible explanation.

TABLE 3.—Average number of *Artemia* in anterior (A) and posterior (P) halves of intestine for each trial.

Time		Density: 1	2	22	66	112
2.5	A	0	15	9	33	300
	P	0	0	0	0	0
5.0	A	0.3	15	108	101	175
	P	0	0	0	0	0
10	A	1.8	50	57	215	467
	P	0	0	0	10	59
30	A	50	51	320	1,077	1,265
	P	0	0	36	327	245
60	A	0.7	165	830	569	
	P	0	45	720	714	
90	A	141	209	890	937	
	P	4	339	385	722	

At 22 *Artemia*/liter the maximum quantity in the intestine is reached at 60 min, and at 66 *Artemia*/liter the maximum is reached at 30 min. Fluctuations in the two halves of the intestine thereafter suggest posterior movement of material and intermittent elimination. This is corroborated by visual observations made during the trials. The earliest detected defecations were at 50 min for the 22 *Artemia*/liter level and at about 30 min for the 66 *Artemia*/liter level. No defecation was detected in the trials at 112 *Artemia*/liter, which did not go beyond 30 min. The quantities in the intestine suggest that rate of movement of material into the posterior part of the intestine approached the maximum at 66 *Artemia*/liter and that defecation might not start any sooner at 112 *Artemia*/liter than at 66 *Artemia*/liter.

From these data it is reasonable to suppose that beyond 30 min the time-specific losses by defecation would be greater for the 66 *Artemia*/liter series than for the 22 *Artemia*/liter series, and negligible for the two lower density levels.

On the supposition that the greatest underestimates of total amounts consumed occurred in the three longest time periods of the 66 *Artemia*/liter series, equation (3) was refitted to

TABLE 4.—Estimated parameter values and 95% confidence limits for density series separately and pooled under particulate and filter feeding.

Artemia/liter	Particulate feeding: Intercept	Particulate feeding: Slope (α)
1	46.8 (−316; 410)	61.5 (53.5; 69.5)
2	181.3 (−1,004; 1,367)	58.5 (45.9; 71.1)
Pooled	0 assumed	60.3 (56.3; 64.3)

Artemia/liter	Filter feeding: Asymptote (N_∞)	Filter feeding: Instantaneous feeding rate (β)
22	20,322 (16,736; 23,908)	0.0052 (0.0031; 0.0074)
66	15,384 (13,991; 16,778)	0.0045 (0.0035; 0.0060)
112	22,050 (16,999; 27,102)	0.0040 (0.0029; 0.0059)
Pooled[1]	23,788 (21,802; 25,775)	0.0036 (0.0032; 0.0042)

[1] The pooled array under filter feeding does not include the 30-, 60-, and 90-min trials for 66 *Artemia*/liter.

the data for the higher density levels with these three trials removed. The estimated parameters are shown, along with those for the lower density levels, and also for the density levels individually, in Table 4. Since the individual series under particulate feeding did not have intercepts that differed from zero, the parameters for the pooled array were estimated with the intercept assumed to be zero. Goodness of fit for the combined data in both density groups was judged satisfactory; in Figure 1 the calculated curves are compared to the standardized trial means and standard errors for each density series. The equations for the two feeding modes can be stated as

$$N_P = 60.3tD \qquad (3)$$

and

$$N_F = 23{,}788\left(1 - e^{-0.0036t\sqrt{D}}\right) \qquad (4)$$

The asymptotic level, 23,788 *Artemia*, is indicative of the maximum capacity of mackerels at an average weight of 147 g. On the basis of the wet weight of *Artemia*, 500 individuals/g, maximum capacity would be 48 g, or 32% of fish weight. This is about double the greatest weight of fish food removed from the esophagus and stomach, but the two kinds of estimate are not necessarily inconsistent. As suggested earlier, the weights of the digestive tract contents may have underestimated the weights of *Artemia* in the live state by 25 to 50% because of digestion and leaching in Formalin. The estimate given here is based on weight of live organisms. Since digestion is going on during protracted feeding,

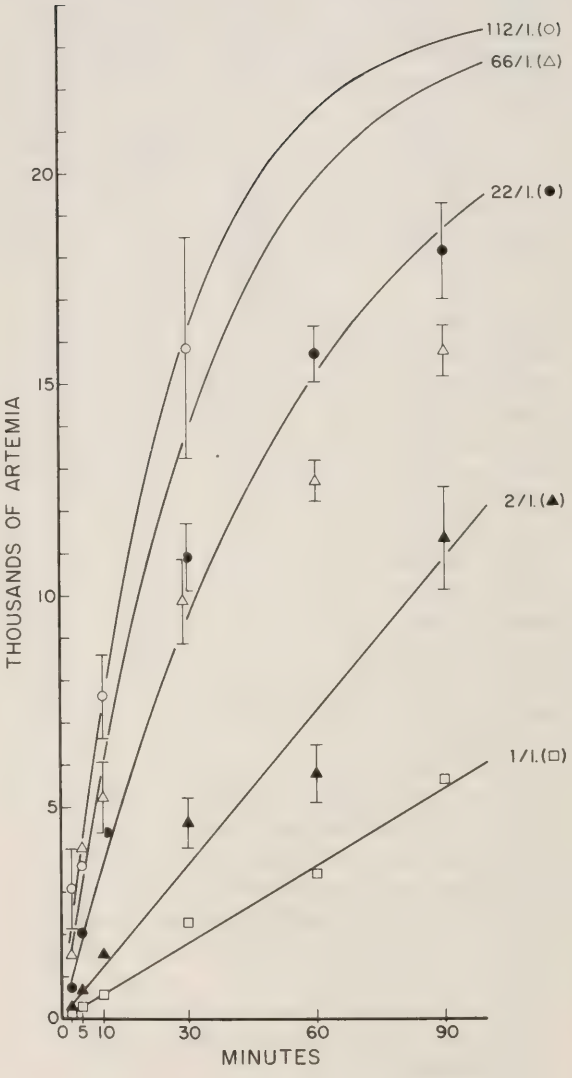

FIGURE 1.—The number of *Artemia* in digestive tracts for different density levels in the water and for different feeding durations. The lines for 1 and 2 *Artemia*/liter were calculated from equation (3) and the lines for 22, 66, and 112 *Artemia*/liter were calculated from equation (4). The symbols associated with each line show averages and standard errors for the trials in that density series. Standard errors smaller than 450 are not shown.

average capacity might well be less than 32% of weight for the asymptotic number specified. The asymptotic number, which was most strongly influenced by the trials at 22 *Artemia*/liter, may slightly underestimate the total number that can be ingested because of losses by defecation.

DISCUSSION

It is evident that *Artemia* adults approximate the smaller crustacean sizes utilized by the mackerel and that the fish resorts to filter feeding to increase the rate of consumption as density exceeds some level where particulate feeding becomes relatively inefficient. The ecological meaning of this feeding pattern is indicated by considering the resulting relation between food density and rate of food accumulation in the digestive tracts in respect to 1) the daily nutritional requirement of the species, 2) the density levels of crustaceans in the sea, and 3) the feeding rates of the northern anchovy (*Engraulis mordax*).

Hatanaka et al. (1957) showed that *S. japonicus* in coastal regions of Japan tend to utilize small fish in late summer and autumn but to rely largely on euphausiids and other crustaceans of similar size in other seasons. They concluded that mackerel a little over 1-year-old and averaging 149 g in weight required 8% of their body weight per day in crustaceans to sustain the growth rate observed in nature, which was estimated as 0.42% of body weight per day. The feeding functions derived in the present study indicate that the times required for the mackerel to obtain this daily requirement at the *Artemia* densities tested, or their equivalent for euphausiids, would be

Artemia/liter	1	2	22	66	112
Euphausiids/liter	0.7	1.3	15	44	75
Minutes	97	49	17	10	7

The equivalent densities for euphausiids are given on the assumption that the mackerel feeding rate is keyed to concentration in terms of biomass rather than to numbers per unit volume as such. Euphausiids near the surface at night in the eastern Pacific, largely *Euphausia pacifica*, average 6 mm in body length (O'Connell, 1971), and individuals of this length are 3 mg wet weight (Lasker, 1966), or 50% more than the *Artemia*.

The feeding times given above are relatively short, but the *Artemia* densities are much higher than those reported for comparable organisms in the sea. Brinton (1962) showed average densities of *E. pacifica*, largely juveniles, to be about 0.02/liter near the surface at night off southern California. O'Connell (1971) showed an average of 0.03/liter over much the same region, with perhaps 5 to 10% of the area having densities approaching 0.1/liter at any one time. These estimates would be elevated, perhaps doubled, if other large crustaceans were added on a biomass equivalent basis. The highest of these area densities would enable the mackerel to obtain its daily nutritional requirement in about half a day of particulate feeding, but the more commonly prevailing level would not permit the mackerel to obtain its requirement within the space of a day.

In all probability the mackerel obtains much of its needs from euphausiids and other crustaceans of similar size, but there is good evidence that it depends to some extent on larger organisms, such as fish up to one-third of its own body length (Hatanaka and Takahashi, 1960), to secure the daily requirement over a reasonable length of time. Though stomachs tended to be fuller and growth better during the season when the mackerel feeds primarily on fish (Hatanaka et al., 1957), it must be remembered that the 8% daily feeding requirement used here pertains to maintenance and growth when euphausiids were the primary food. If the feeding rates indicated for higher densities of *Artemia* apply for biomass equivalents of much larger organisms, the large capacity of the mackerel suggests that relatively infrequent encounters with such organisms would sustain the daily requirement in an average sense. The present study and that of Kariya and Takahashi (1969) indicate that feeding can be expected to continue towards full capacity regardless of state of fullness when food becomes available.

Though mackerel may have to depend in part on larger organisms, it is possible that the food

potential of the larger crustaceans, and even very young fish, is greater than indicated by average area densities. The definite filtering response of the mackerel, which appears to be an adaptation for capturing the smaller organisms it utilizes at a greater rate than would be possible by biting activity when density is high, implies that high densities are a factor of some consequence in the feeding ecology of the species. One possible explanation is that the various kinds of food organisms tend to be distributed contagiously, with aggregations of considerably higher density than reflected by area averages. As Ivlev (1961) demonstrated with carp fry, feeding rate can be expected to increase with degree of aggregation for a fixed quantity of food organisms. Euphausiids have been observed in schools and breeding swarms (Brinton, 1962). More than likely the filtering response is evoked in mackerel with empty or near-empty stomachs by densities not much above the equivalent of 1 or 2 *Artemia*/liter, where rate of effective biting must already be on the order of 60 or more per minute. At 4 to 5 *Artemia*/liter the daily nutritional requirement could be obtained in less than 45 min of filter feeding.

Whereas *Artemia* adults represent the smallest organisms consumed by the mackerel, they represent the largest organisms commonly consumed by the anchovy (Loukashkin, 1970); the latter also consumes phytoplankton and crustaceans less than 1 mm in length by filter feeding. The wet weight quantities of *Artemia* adults consumed at different densities (Table 5), based on the present study for the mackerel and on Leong and O'Connell (1969) and O'Connell (1972) for the anchovy, suggest the differences in utilization and nutritional value of large crustaceans for equivalent age groups of the two species.

The anchovy requires far less food than the mackerel to meet its daily nutritional requirement, and can obtain the necessary quantity in about 20 min when *Artemia* adults are at densities of 1 or more per liter. In this same period the mackerel consumes more than the anchovy at all densities, but not enough to satisfy the daily requirement. When considered in terms of the weight of the two fish, the greater quantities consumed by the mackerel have a relatively lower nutritional value than those consumed by the anchovy, except, perhaps, at very high densities.

TABLE 5.—Comparison of *Artemia* adults consumed (mg wet weight) by the 1-year-old mackerel and anchovy for different density levels of *Artemia* in the water.[1]

Item	Mackerel	Anchovy
Age in years	1+	1–
Weight ± g	147	4
Nutritional requirement:		
Percent body weight	8	6.8
mg	11,784	270
Minutes of feeding for nutritional requirement at:		
1 *Artemia*/liter	97	20
5 *Artemia*/liter	35	20
Mg *Artemia* consumed in 20 min with *Artemia* at:		
0.1 *Artemia*/liter	240	~152
1 *Artemia*/liter	600	270
5 *Artemia*/liter	9,600	270
Mg *Artemia* consumed/g fish weight in 20 min with *Artemia* at:		
0.1 *Artemia*/liter	1.6	~38
1 *Artemia*/liter	17	68
5 *Artemia*/liter	65	68

[1] Calculations for the anchovy at age 1+ and weight 7 g show the nutritional requirement and amounts consumed in 20 min at 1 and 5 *Artemia*/liter to be 475 mg, but all other values are the same as for the 4-g anchovy.

The extreme difference in quantities consumed by the two species at high densities is attributable to the filtering capability of the mackerel, and the failure of the anchovy to filter feed on the larger crustaceans, regardless of density. No meaning can be attached to the small difference at the lowest density level because calculation of the values involved considerable extrapolation. It is nevertheless probable that the anchovy tends to remove large crustaceans at a lower rate than the mackerel at such levels. O'Connell (1972) showed that the feeding activity of the anchovy is likely to be divided between these and the smaller crustaceans captured by filtering if the larger organisms are less than about 5 to 8% of the dry weight of total zooplankton concentration.

From the above considerations it is tentatively hypothesized that the individual mackerel generally utilizes a greater proportion of the large crustaceans in the sea than does the individual anchovy, but that the proportion utilized generally has a relatively low nutritional value for the mackerel.

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COLOR PATTERNS OF SPINNER PORPOISES (*STENELLA* CF. *S. LONGIROSTRIS*) OF THE EASTERN PACIFIC AND HAWAII, WITH COMMENTS ON DELPHINID PIGMENTATION

WILLIAM F. PERRIN[1]

ABSTRACT

In this paper, the second of a series on the morphology of small pelagic delphinids by the author, the color patterns of forms of a tropical spinner porpoise *Stenella* cf. *S. longirostris* (Gray) 1828 from the far eastern Pacific, from the waters between North America and Hawaii, and from Hawaiian waters are described and illustrated. The patterns can be analyzed in terms of discrete component systems, and most geographical variation appears to be in a "dorsal field system" overlying a basic general pattern. The overlay is darkest and most extensive in the easternmost form considered and lightest and least extensive in the Hawaiian form. The color patterns of three other delphinids, *Stenella graffmani*, *Delphinus* sp., and *Tursiops truncatus* are analyzed with the component approach, and possible pattern element homologies are defined.

During the course of collecting materials and data for population studies of porpoises involved in the seine fishery for tunas in the eastern tropical Pacific (Perrin, 1970a), I have during the last several years had the opportunity to observe and, less often, to photograph the color patterns of a large number of small pelagic delphinids of several species. Emerging patterns of variation and their possible implications for the systematics of these very poorly known mammals have prompted me to undertake detailed analyses of this body of observations. I have previously (Perrin, 1970b) described the color pattern of the eastern Pacific spotted porpoise *Stenella graffmani* (Lönnberg) 1934. The primary purpose of this paper is to describe the ontogeny and geographical variation of the color patterns of spinner porpoises of the eastern tropical Pacific and Hawaii. Some description is included also of variation in the shape of the dorsal fin and correlated features.

The study is based on observations on 157 specimens from the eastern Pacific (Figure 1), of which 41 were photographed, and on photographs and observations of approximately 35 wild and captive animals from Hawaiian waters. Many of the specimens, including most of those from the far eastern Pacific east of Clipperton Island, were examined minutes after capture; others were examined after being held in frozen storage for up to 8 months. Degree of sexual development was determined by histological examination of gonads, with the exception of the large male (Figure 8) from Acapulco, of which only a photograph is available and which was undoubtedly a mature male. Skeletons of specimens of many of the animals illustrated were placed in museums, and the museum numbers are given in the figure captions.

The spinner porpoise of the far eastern Pacific has been referred to *Stenella microps* (Gray) 1846 (Miller and Kellogg, 1955; Hester,

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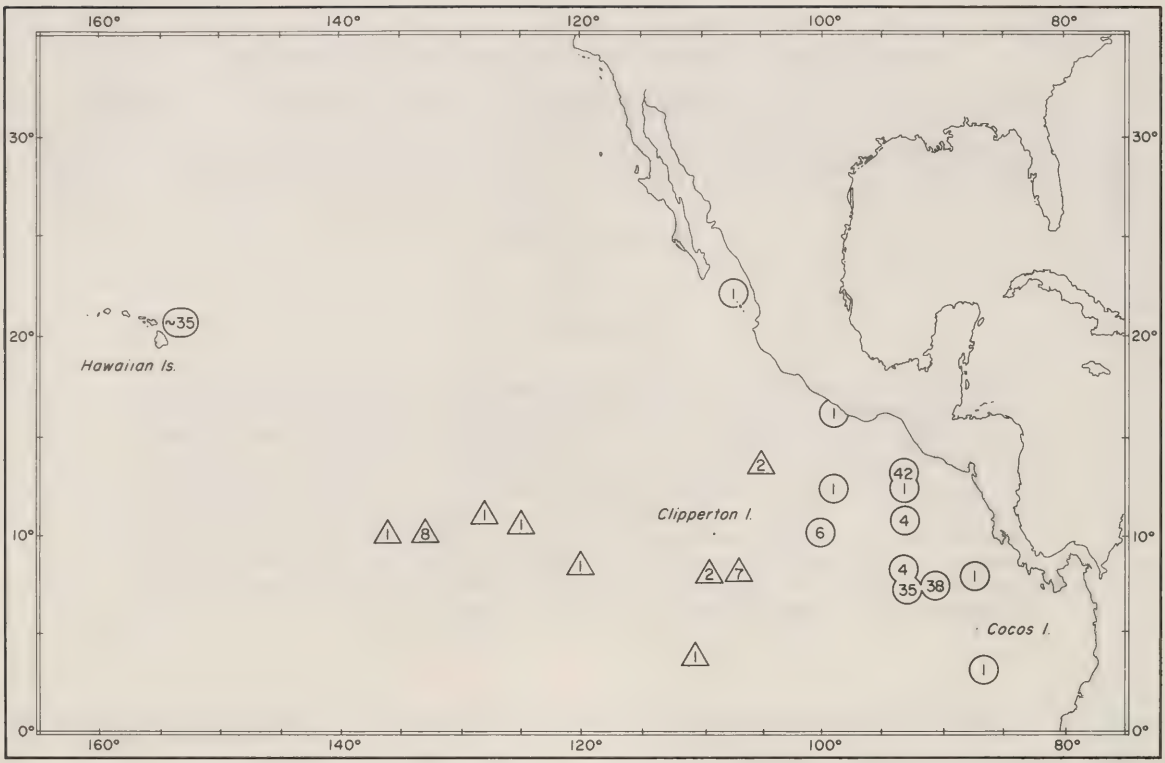


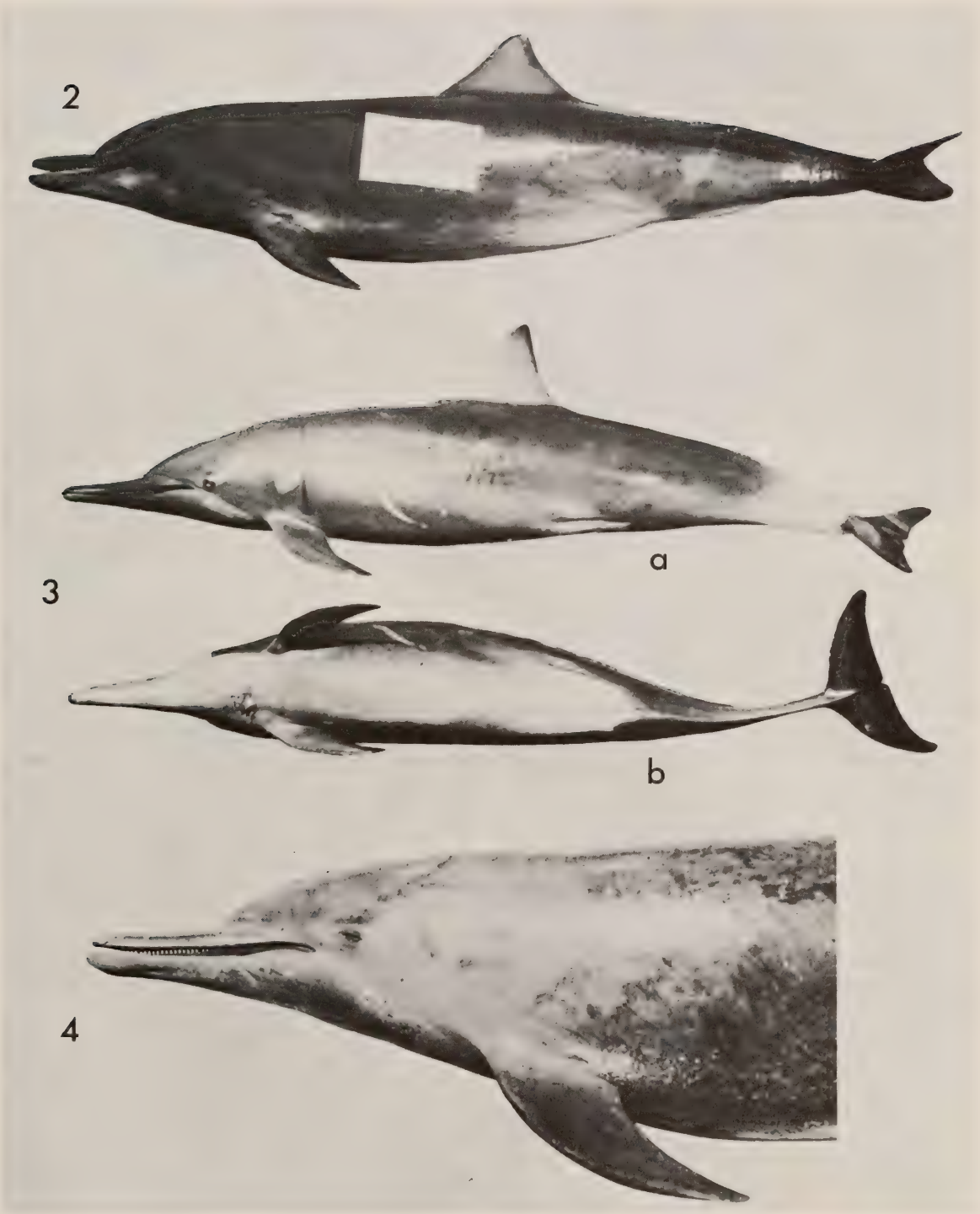
FIGURE 1.—Localities and numbers of specimens examined. Circles in eastern area indicate "eastern spinners"; triangles indicate "whitebelly spinners."

Hunter, and Whitney, 1963; Nishiwaki, 1967; Pilson and Waller, 1970), but others regard *S. microps* as a synonym of *S. longirostris* (Gray) 1828 (Hershkovitz, 1966; Rice and Scheffer, 1968; Harrison, Boice, and Brownell, 1969). The spinner porpoise of Hawaii has been referred to *S. longirostris* (Hershkovitz, 1966; Nishiwaki, 1967; Tomich, 1969) and to *S. roseiventris* (Wagner) 1853 (Brown, Caldwell, and Caldwell, 1966; Fraser, in Morris and Mowbray, 1966; Rice and Scheffer, 1968). The type localities for *S. microps* and *S. longirostris* are unknown; *S. roseiventris* was described from the Banda Sea, Indonesia. The spinner porpoise of the far offshore areas of the eastern Pacific—called "whitebelly spinner" by fishermen—has not to my knowledge been previously described or referred to any named species. No critical review of the

FIGURE 2.—Calf of eastern spinner. Male, 105 cm total length, from lat 10°30'N, long 92°56'W, April 4, 1968. Perrin field no. CV83; specimen not saved. Shape of dorsal fin is distorted by angle of photograph, should be higher. Photographed minutes after death.

FIGURE 3.—Lateral (a) and ventral (b) views of subadult eastern spinner. Female, 166 cm, from 21°43'N, 106°47'W, February 17, 1967. Marine Mammal Biological Laboratory (Seattle) field no. 1967-102. Skeletal specimen in MMBL collection. Photographed minutes after death.

FIGURE 4.—Adult eastern spinner. Female, 166 cm, from 12°51'N, 93°18'W, April 9, 1968. Perrin field no. CV7; specimen not saved. Photographed minutes after death.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genus has been accomplished since True's work on the Delphinidae published in 1889, when the existence of spinner porpoises in eastern Pacific and Hawaiian waters was not yet known. Evidence presented below concerning geographical variation in pigmentation supports the concept of a single species, highly variable geographically, but taxonomic and nomenclatorial decisions must be based on adequate review of osteological characters, as well as on a broader range of external characters than is considered here. The use of *Stenella* cf. *S. longirostris* therefore is provisional pending the outcome of more extensive studies underway by me and others. A similar situation obtains for the spotted porpoises, and use here of *Stenella graffmani* for the spotted porpoise(s) of the eastern Pacific is also provisional.

DEVELOPMENT AND INDIVIDUAL VARIATION

This account of ontogeny is divided into two parts, one describing development of color pattern as inferred from specimens from the more easterly, relatively nearshore population(s) of spinner porpoise referred to below as the "eastern spinner," and another for specimens of the "whitebelly spinner" of the more westerly, farther offshore areas of the eastern Pacific (Figure 1).

EASTERN SPINNER

Length at birth is 75 to 85 cm (Harrison et al., 1969). The smallest specimen examined was 80 cm long. The smallest specimen photographed was 105 cm long (Figure 2). At this size, the animal is predominantly dark gray. The gray of the dorsum grades imperceptibly into white around the genital region and in a smaller area in the axillary region. A dark gray flipper band from flipper base to the eye-gape region is demarcated above by a narrow, very light line running from behind the posterior insertion of the flipper to the eye and below by a sharp boundary with a light gray gular region. The boundary between the two shades of gray runs forward between the eye and the end of the gape, becoming obscure in the furrow at the base of the melon. The very light gray below grades anteriorly into darker gray, so that the upper and lower sides of the snout are of about the same shade as the dorsal field. The gape is edged with very dark gray sharply delineated above for about the last third of the gape and below for about the last half of the gape but grading distally above and below into the generally dark gray of the snout. A small eye patch of similar shade is present, and a narrow eye stripe, also of dark gray, runs from the eye patch forward to join the gape mark near the apex of the melon. A similar mark extends from the blowhole to the apex. The margin of a very faintly defined dorsal cape (not visible in the photographs) runs from near the apex of the melon to behind the dorsal fin, passing high over the eye and dipping slightly below the fin to yield a saddle effect discernible only upon very careful scrutiny of a freshly caught animal. Low on the side and adjacent to the genital slit, an elongate, smudge-like mark extends obliquely for several centimeters along a line that if extended in both directions would run from the eye to behind the anus. All appendages are on both surfaces the same gray as the dorsum. The major point of individual variation in animals of this and larger size is in the extent of the ventral and axillary white areas; in some individuals they are larger and may even be confluent, with the dorsal margin extending back from the axillary area to run into the higher genital white area.

The pattern persists as described into subadulthood (subadult being defined as an animal of adult or near-adult size but sexually immature) without change aside from overall darkening (Figure 3). In subadulthood the margins of the ventral and axillary white areas begin to become speckled, and in adults (Figures 4, 5, 6, 7, 8, and 9) the dorsal field, by now very dark gray, appears to encroach on the white areas with spots and blotches to yield a very speckled appearance below (Figure 10). As in younger animals, the major feature subject to individual variation appears to be the extent of the white areas, although in no adult specimens examined were the genital and axillary areas confluent.

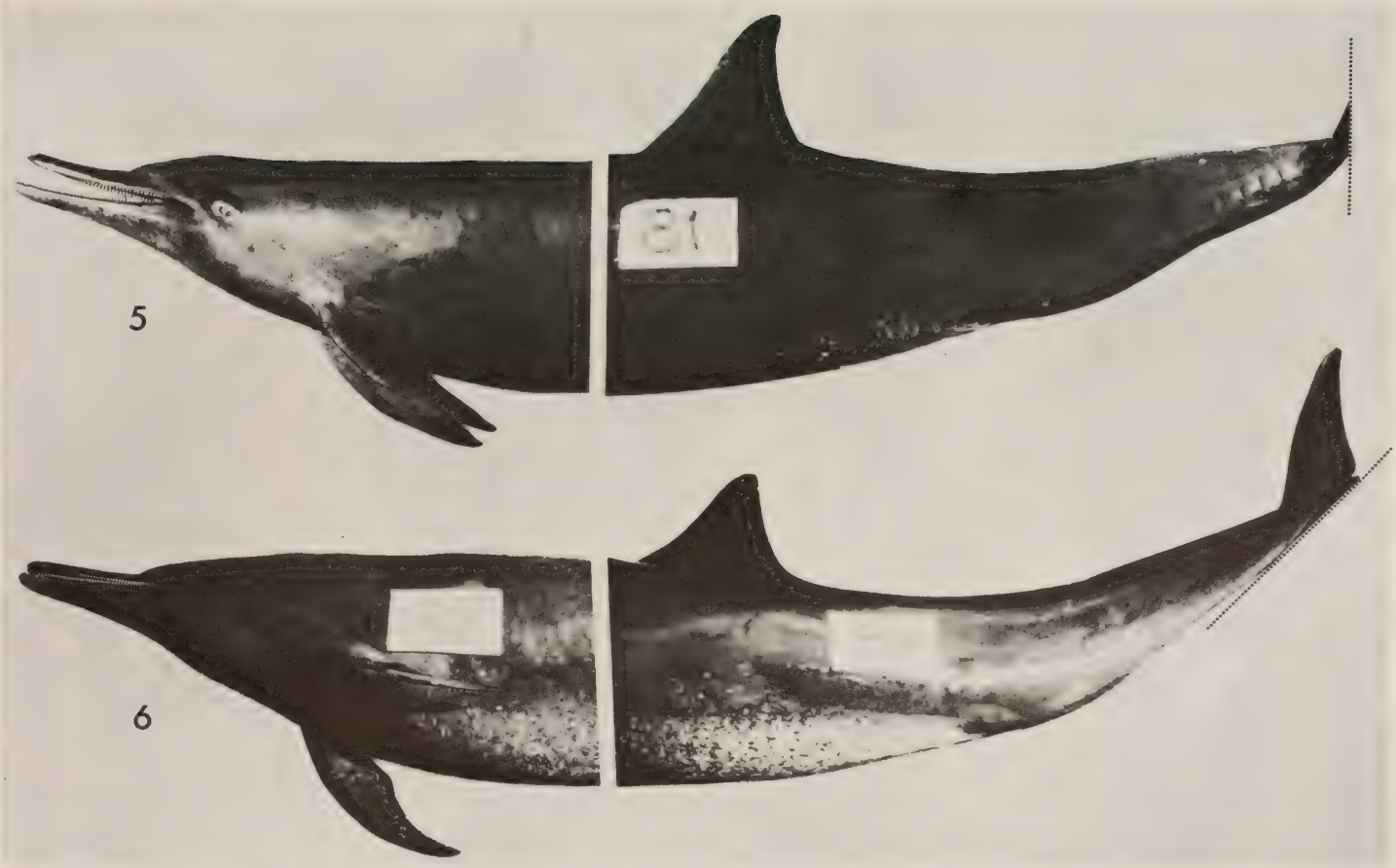


FIGURE 5.—Adult eastern spinner. Female, 160 cm, from 10°30′N, 92°56′W, April 12, 1968. Perrin field no. CV81; specimen not saved. Photographed minutes after death.

FIGURE 6.—Adult eastern spinner. Female, 169 cm, from 10°30′N, 92°56′W, April 12, 1968. Perrin field no. CV82; specimen not saved. Photographed minutes after death.

In the specimens with largest white areas, the region corresponding to that of confluence in some younger specimens was dark gray thickly peppered with light gray spots (Figure 6). In some adults, the gular area is also flecked with light spots (Figure 4). In all adults the degree of contrast between the flipper band and the gular region is much reduced over that in younger animals. The cape remains obscure (see photograph of specimens in water in Perrin, 1968). The oblique mark adjacent to the genital region is obliterated in most adults, but in some can still be faintly discerned (Figure 6). The thin light gray line delineating the upper margin of the flipper band may in adults be prominent or so faint as to appear absent.

In adult males, the dorsal fin is canted forward to a greater or lesser degree (Figures 7, 8, and 9). Development of this feature is correlated with development of a protuberant keel, composed of connective tissue, just posterior to the anus. The function of these features is unknown. However, comparison of the habits of this spinner with those of the Hawaiian spinner, in which the features are very weakly developed (see below), provides a basis for a deductive hypothesis. In the eastern Pacific, spinners commonly occur together with spotted porpoise (*S. graffmani*) in mixed schools comprised of several hundred, or even thousands, of individuals of each species. In Hawaiian waters, spinners and spotted porpoise [there referred to *S. attenuata* (Gray)] do not occur in mixed schools (personal communication from K. S. Norris). In Hawaiian waters, then, most interspecific contacts could be assumed to be head-on and made at some distance, while in the mixed schools of the eastern Pacific interspecific contacts must be relatively more frequent, made at shorter distances, and for the most part lateral. It can be hypothesized that the features function in species recognition in a sexual context, perhaps, for example, to insure that oestrous females make advances to males of the proper species.

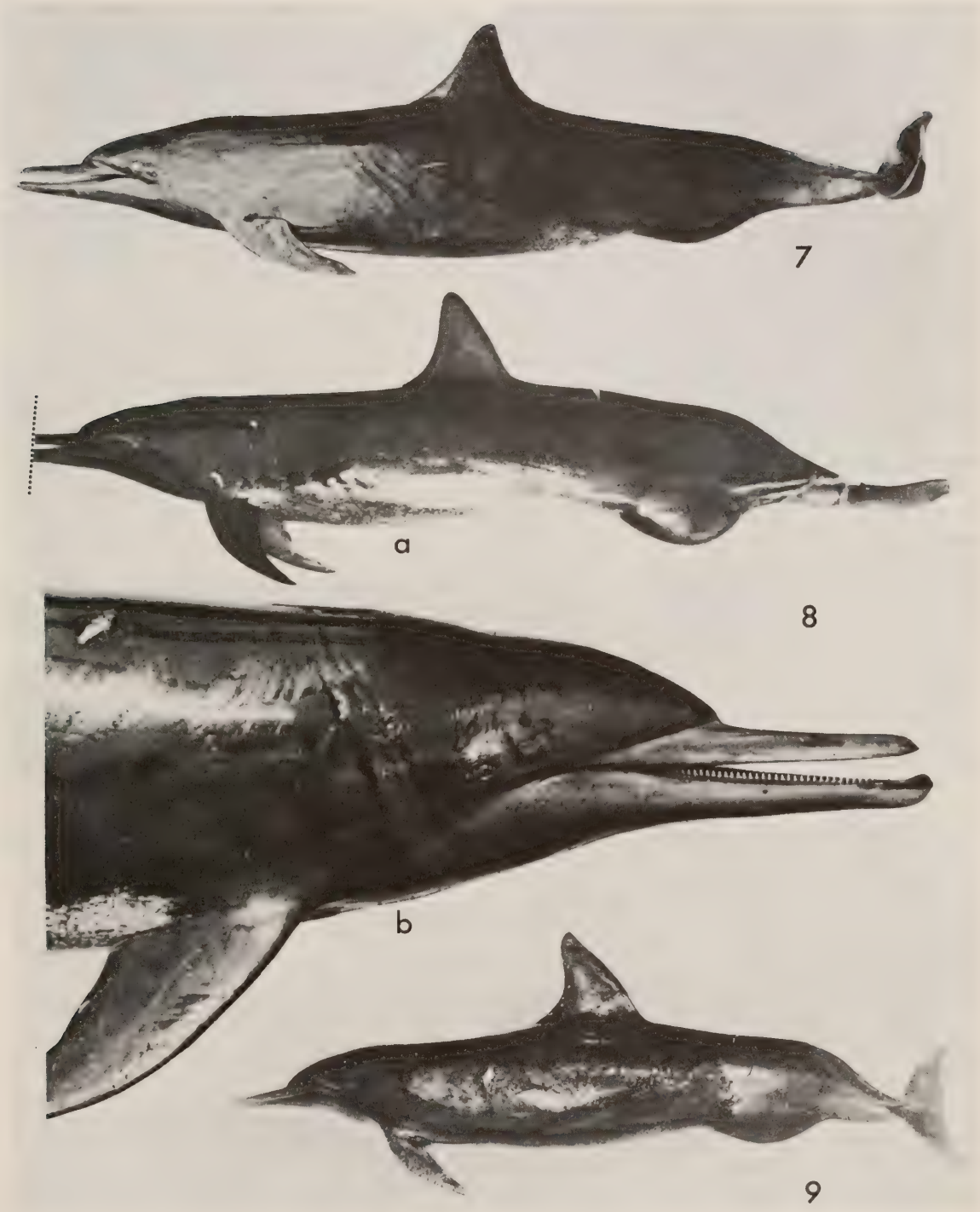
FIGURE 7.—Adult eastern spinner. Male, 175 cm, from 3°N, 87°W, July 19 or 20, 1970. Perrin field no. WFP47; U.S. National Museum no. 396026 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 8a and b.—Adult eastern spinner. Male from off Acapulco, Mexico. Photographed soon after death. Specimen not saved.

FIGURE 9.—Adult eastern spinner. Male, 186 cm, from 12°20'N, 92°53'W, March 10, 1968; San Diego Natural History Museum no. 21427 (complete skeleton and cast). Photographed in frozen state after several months in frozen storage.

WHITEBELLY SPINNER

In this animal the ventrum is white. In all young specimens examined, the axillary and genital white regions were confluent (Figure 11) as in only some young eastern spinners. Again, not much change occurs in the pattern until late subadulthood (Figures 12, 13, and 15) when the margin of the ventrum becomes speckled. The main point of difference between these animals and the eastern specimens, aside from the larger ventral light areas, is that there is much greater contrast between the dorsal cape and the lateral field. The cape can even be discerned in some of the photographs of frozen specimens (Figure 13). In some subadults (Figure 13) an anteriorly narrowing dark gray mark can be seen in the area between the flipper insertions. Other differences between this and the eastern form are discussed below. As in the eastern spinner, individual variation among adults (Figures 16, 17, 18, 19, 22, and 23) is most pronounced in extent of the light ventrum, but the lower end of the range is about equal to the upper end for the eastern spinner. Also again, there is considerable variation in intensity of speckling (compare Figures 16 and 22), and the supra-flipper-band stripe may be effectively absent (Figure 19). The flippers are usually dark on both sides, but may be speckled above (Figure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22) and/or below (Figure 21). The oblique mark adjacent to the genital region is obliterated in some adults, but in others (Figure 23) is very clearly delineated.

FIGURE 10.—Close view of genital region of adult male eastern spinner depicted in Figure 9.

FIGURE 11.—Lateral (a) and ventral (b) views of calf of whitebelly spinner. Female, 105 cm, from 8°N, 109°45'W, March 5, 1969. Perrin field no. PQ11; U.S. National Museum 395601 (complete skeleton). Photographed frozen after approximately 1 month in frozen storage.

FIGURE 12.—Subadult whitebelly spinner. Female, 129 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP58; U.S. National Museum 396036 (complete skeleton). Photographed after frozen for several months and thawed in water.

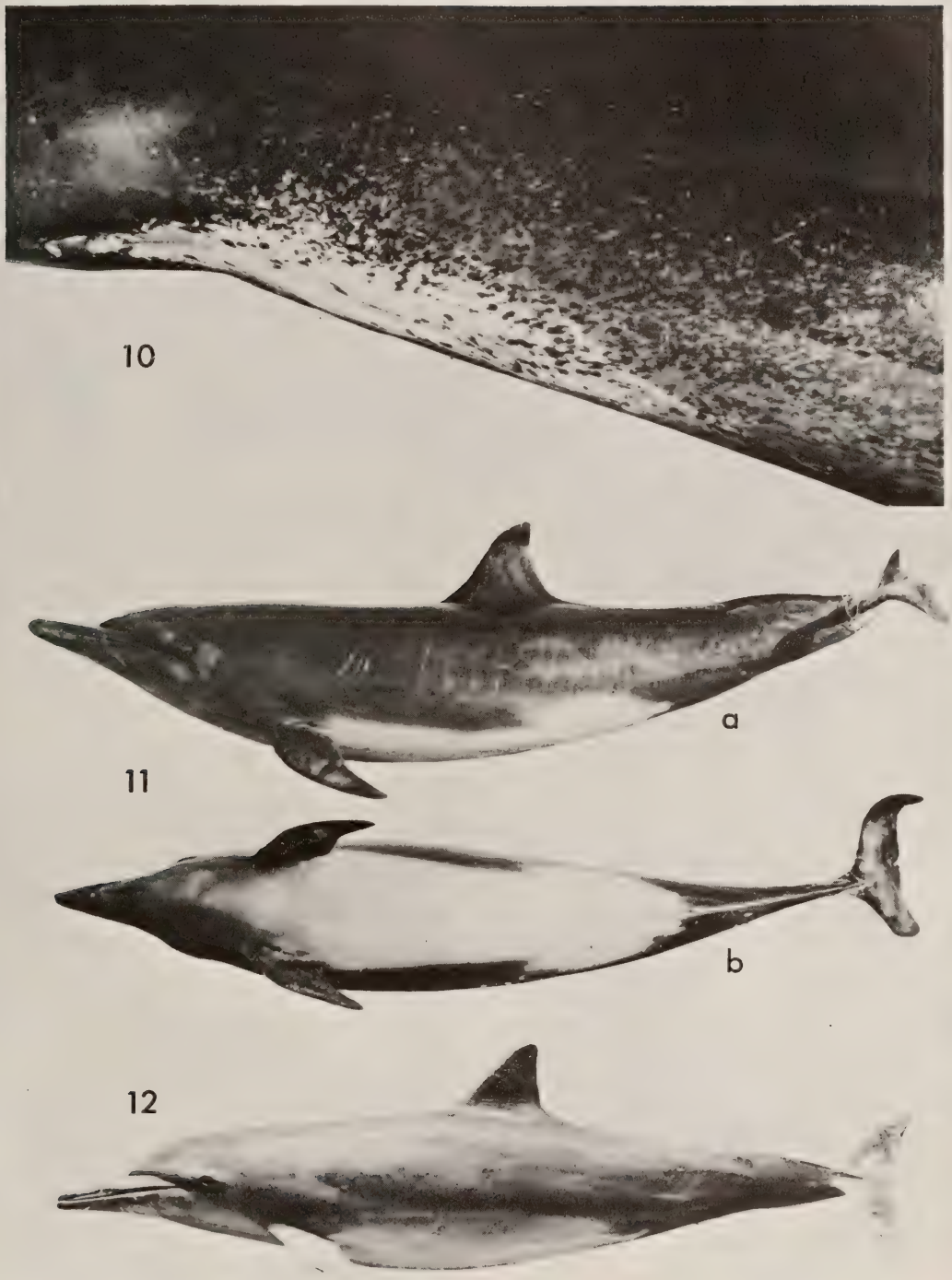
GEOGRAPHICAL VARIATION

Very young specimens of the Hawaiian spinner (Figure 24, and Figure 7 in Perrin and Hunter, 1972) were not available for examination nor was it possible to determine with certitude the degree of maturity of most of the animals seen. One large male observed (PUKA at Sealife Park in Waimanalo, Oahu), however, has been in captivity for 5 years and can be presumed to be adult. The major differences between the Hawaiian spinner and the whitebelly spinner of the eastern Pacific are that in the Hawaiian animal the light ventrum extends dorsad nearly to the level of the eye, as it does in its extreme expression in the whitebelly spinner, and is not speckled at the margin. The dorsal fin becomes increasingly erect with development, but is always at least slightly falcate, and the ventral keel associated with triangular and canted fins in the eastern Pacific spinners is all but absent. All contrasts are on the average more pronounced: between cape and lateral field, flipper band and gular area, gape mark and underside of lower jaw. The ventral margin of the cape follows a convex smooth curve over the eye in the whitebelly spinner but dips over the eye in the Hawaiian form.

The differences among the whitebelly, eastern, and Hawaiian spinners are summarized in Table 1. These differences appear to be based primarily in differential development. The small subadult of the whitebelly spinner (Figures 12 and

TABLE 1.—Summary of some external features differing between adults of Hawaiian, whitebelly, and eastern spinner porpoise.

Feature	Hawaiian spinner	Whitebelly spinner	Eastern spinner
Contrast of cape with lateral field	Very pronounced	Clearly discernible	Effectively absent
Ventral margin of cape over eye	Dips	Smooth curve, no dip	Obscure
Ventral white field	Extends dorsad nearly to level of eye; margin smooth	Extends dorsad variably nearly to level of eye; margin speckled; genital and axillary areas confluent	Restricted to discrete genital and axillary areas of varying extent; margins speckled
Black snout tip	Present	Variable	Absent
Contrast between flipper band and gular region	High	High to medium	Low
Spots in gular region	Absent	Variable	Variable
Flippers	Dark	Dark or speckled	Dark
Dorsal fin in adult male	Falcate	Falcate to triangular	Triangular to canted
Protuberant ventral keel in adult male	Absent	Small to medium	Small to large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13) more closely resembles the Hawaiian spinner than does the adult, in that the margin of the ventral white field is relatively smooth. The pattern of the fetus of the eastern spinner (Figure 25) is also very close to the Hawaiian pattern, with the tripartite effect of cape, lateral field, and high ventral field being very pronounced. The question of which sort of developmental cline is involved, paedogenesis to the west or gerontogenesis to the east, is however yet an open one and must be settled by consideration of additional lines of morphological and zoogeographic evidence.

Pattern component analysis.—Comparison of the color pattern of a partially albinistic subadult whitebelly spinner (Figure 14) with that of a normally pigmented individual of the same sex and nearly the same length (Figure 13) affords insight into the mechanisms of pattern formation. In the lighter-than-normal animal, the cape, eye patch and stripe, gape mark, dorsal fin, and flukes are as in the normal specimen. The lateral field, flipper band, and oblique genital mark are obscure, and the flippers are white on both surfaces. White brushings sweep up from the edge of the cape at about midlength toward the dorsal fin. From these facts, the inference can be made that the full normal pattern is the result of the combined effect of two independent pigmentation systems, one involving the cape and accessory stripes, eye and gape marks, dorsal fin, and flukes, and the other involving lateral field, flipper band, and flippers. While the genital mark is not apparent in the albinistic animal, the developmental pattern of obliteration through development of the lateral field suggests that it belongs to the cape system. The difference among the Hawaiian, whitebelly, and eastern spinners can be interpreted schematically in terms of these hypothetical systems (Figure 26), allowing a clearer picture to emerge of the possible patterns of geographical variation involved. Since the lateral field appears in this sense to be the lateral portion of a more extensive dorsal field overlaying the cape, it is referred to below as an aspect of a "dorsal field overlay."

Among these three forms, the "dorsal field overlay" is darkest and most extensive in the easternmost form, and least so in the Hawaiian form. It is not yet known whether the three forms represent modes in a geographically continuously varying single species or two or more reproductively isolated allopatric or sympatric populations.

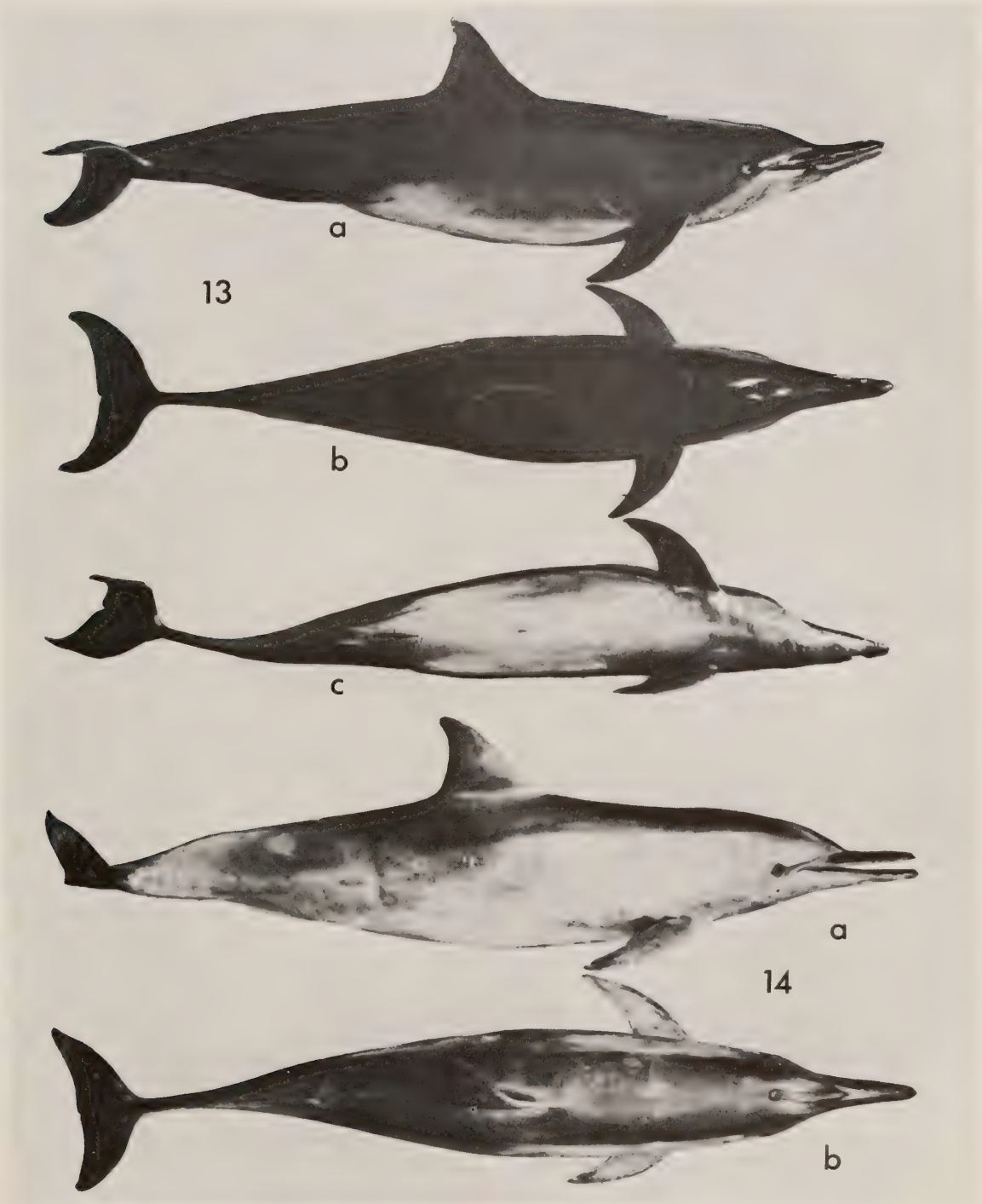
FIGURE 13.—Lateral (a), dorsal (b), and ventral (c) views of subadult whitebelly spinner. Male, 164 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP65; U.S. National Museum 396017 (complete skeleton). Rostrum damaged. Photographed after frozen for several months and thawed in water.

FIGURE 14.—Lateral (a) and dorsal (b) views of albinistic subadult whitebelly spinner. Male, 154 cm, from 10°19'N, 135°38'W, August 5, 1970. Perrin field no. WFP67; U.S. National Museum 396020 (complete skeleton). Compare with normally pigmented animal in Figure 13. Note dark flukes and light flippers. Photographed after frozen for several months and thawed in water.

OTHER DELPHINIDS

The color patterns of other closely related delphinids can be similarly dissected into hypothetical component systems. The patterns of three forms of which I have directly examined live or freshly captured dead specimens are analyzed in Figure 27, with an attempt to define possible homologies for the component systems among the species. As the first step in breaking down the patterns into supposedly homologous components, I attempted to define for each a cape with associated markings, similar to that in the albinistic spinner described above.

In the eastern Pacific spotted porpoise, *Stenella graffmani*, (Figure 27, top) the general cape system is very close to that of the spinners, with the cape extending farther ventrad. The dorsal overlay is less extensive than in any of the spinners, and the flipper band runs forward to the gape rather than to the eye. The area of contact between the flipper band and the gape mark in this and in similar spotted porpoise from other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parts of the world is emphasized in many individuals by a zone of lighter pigmentation (see Figures 4 and 6 in Perrin, 1970b; Figure 1 in Best, 1969; and Figure 3 in Nishiwaki, Nakajima, and Kamiya, 1965), which supports the idea of separate origin of the two marks. In the spotted porpoises, the combined pattern systems are overlaid with discrete dorsal and ventral spot systems that to greater or lesser extent obliterate them (Perrin, 1970b).

In *Delphinus* spp. (Figure 27, middle) the dorsal field overlay is less extensive anteriorly than the cape, resulting in invasion of the cape by the ventral field and yielding a four-part criss-cross pattern with zones of black, buff, gray, and white. The deduction to be made is that the whitebelly region represents total lack of pigment, the buff "thoracic patch" (terminology of Mitchell, 1970) represents the color yielded by the pigment of the cape alone, the gray "flank patch" (of Mitchell) that of the pigment of the dorsal field overlay alone, and the black dorsalmost area that of the combined effect of the pigments of the cape and the dorsal field overlay. Chromatographic analysis of pigments present in the various regions and comparison of the results with those of similar tests for other delphinids would contribute to verification or rejection of the suggested homologies.

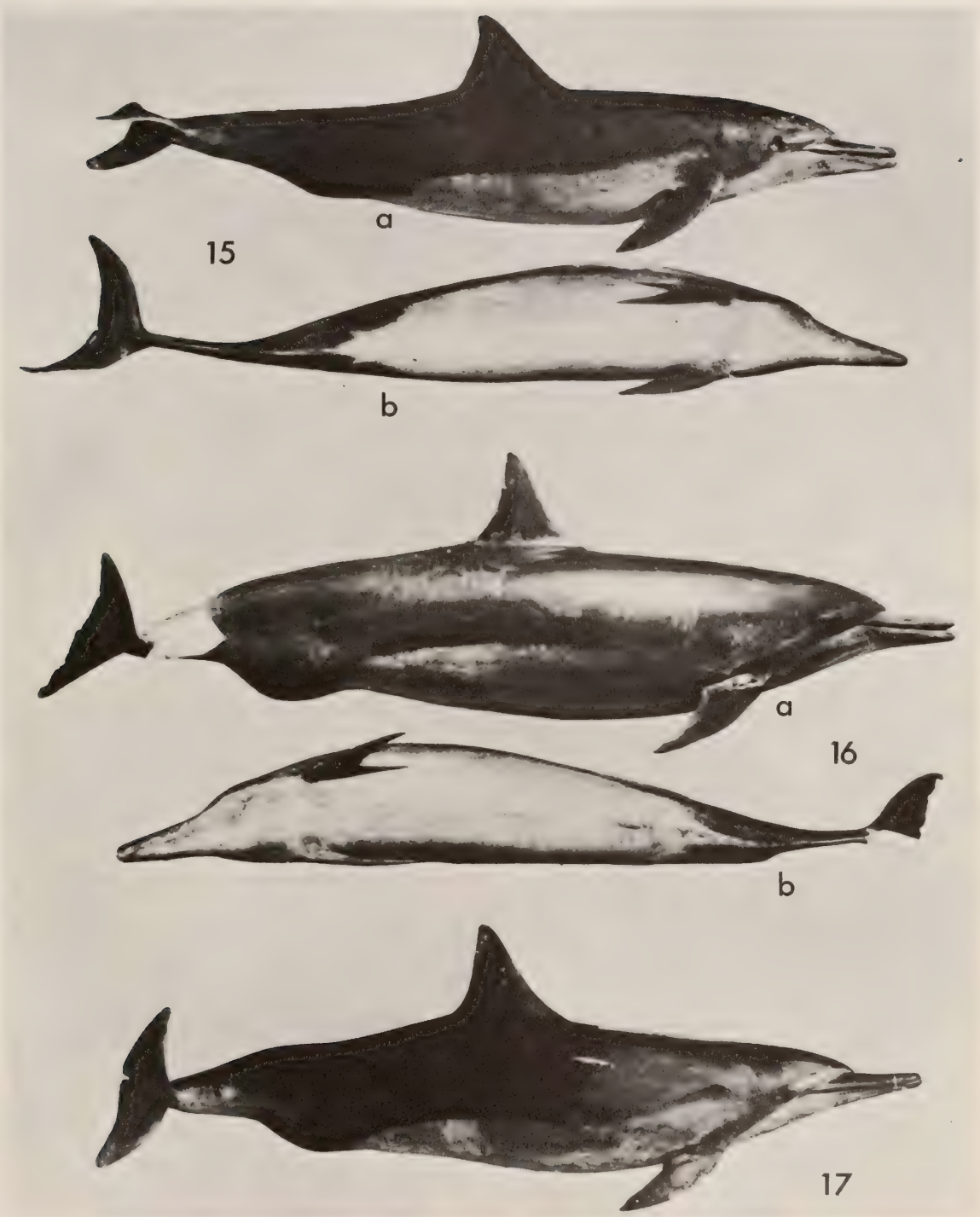
The pattern of *Tursiops truncatus* (Figure 27, bottom) is very close to that of the spinners in every respect, with the flipper band running to the eye and demarcated dorsally by a narrow light line. The dorsal field overlay of varying darkness extends ventrad to about the same degree as in the eastern spinner. Observation of wild bottlenose porpoise in the eastern temperate and tropical Pacific and examination of some of the thousands of published photographs of animals from around the world lead me to believe that the main component of geographical variation, as for the spinner porpoises, is the extent and darkness of the dorsal overlay. In Hawaiian *Tursiops* that I have observed, the ventral margin was high and sharply defined exactly as in the Hawaiian spinner.

The general cape system common to the four forms discussed above corresponds roughly to the "saddled pattern" described by Mitchell (1970) as a generalized and probably primitive pattern within the Delphinidae. The "saddled pattern" depicted in his Figure 7, however, is definitely not that of the spinner porpoises, which he included in a group of "saddled" species in his Figure 17. I concur with Mitchell in his selection of the "saddled" condition as a good candidate for a primitive pattern, insofar as his definition of that pattern category pertains to the "general cape system" described here. Lines of evidence presented here leading to this conclusion are the possession in common of a relatively invariant cape system by several delphinid species and the tendency of the cape to be partially marked, distorted, or obliterated in a varying fashion within a species or species group not so much by alteration of its intrinsic form but more by interaction with more plastic overlying systems or (as Mitchell pointed out in the case of the "spinal blaze") by subtraction through invasion by areas of nonpigmentation.

FIGURE 15.—Lateral (a) and ventral (b) views of subadult whitebelly spinner. Male, 166 cm, from 10°N, 129° or 136°W, August 10-12, 1970. Perrin field no. WFP71; U.S. National Museum 396023 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 16.—Lateral (a) and ventral (b) views of adult whitebelly spinner. Male, 169 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP53; U.S. National Museum 396031 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 17.—Adult whitebelly spinner. Male, 174 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP76; U.S. National Museum 396170 (complete skeleton). Photographed after frozen for several months and thawed in water.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Specimens were collected and examined through the cooperation of the owners, captains, and crews of the tunaboats *Carol Virginia, Conte Bianco, Connie Jean, Conquest, Anne M, Pacific Queen,* and *Queen Mary.* C. J. Orange, J. S. Leatherwood, and G. D. Sharp collected specimens. D. W. Rice provided the photographs used in Figure 3. J. H. Prescott provided photographs used in Figure 8. K. S. Norris provided photographs used in Figure 24, and arranged for a visit to Hawaii to observe wild and captive spinner porpoise. I am indepted to Bonnie Dalzell for the ideas concerning the possible significance of the canted fin and ventral keel in the eastern spinner. K. S. Norris, E. D. Mitchell, D. W. Rice, C. O. Handley, Jr., and D. K. Caldwell read the manuscript. E. D. Mitchell offered especially valuable criticism.

FIGURE 18.—Adult whitebelly spinner. Male, 177 cm, from 9°47'N, 133°25'W, August 11, 1970. Perrin field no. WFP54; U.S. National Museum 396032 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 19.—Adult whitebelly spinner. Male, 178 cm, from 10°N, 128° or 136°W, August 10-12, 1970. Perrin field no. WFP52; U.S. National Museum 396030 (complete skeleton). Photographed after frozen for several months and thawed in water.

FIGURE 20.—Dorsal surface of flipper of specimen depicted in Figure 17.

FIGURE 21.—Ventral surface of flipper of specimen depicted in Figure 19.

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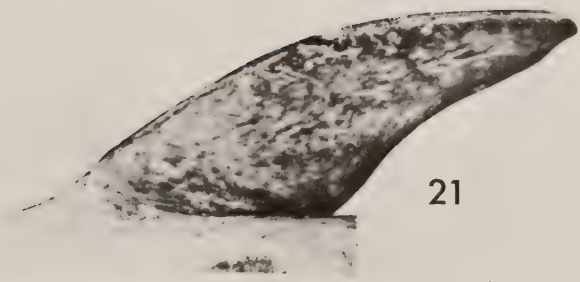

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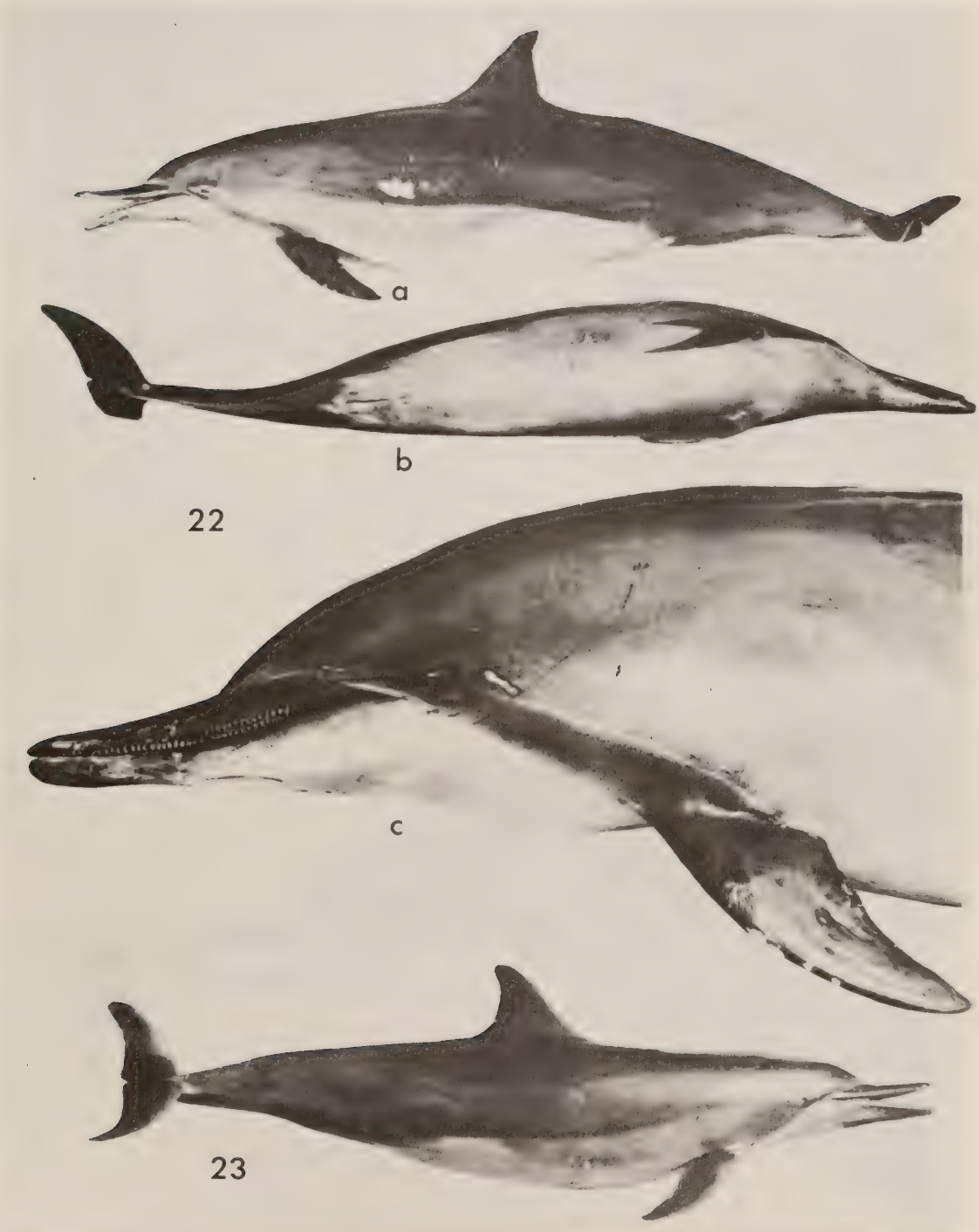
FIGURE 22.—Lateral (a) and ventral (b) views of adult whitebelly spinner. Female, 179 cm, from 3°20′N, 110° 44′W, June 24, 1970. Perrin field no. WFP79; U.S. National Museum 396173 (complete skeleton). Rostrum damaged. Photographed after frozen for several months and thawed in water.

FIGURE 23.—Adult whitebelly spinner. Female, 169 cm, from 8°19′N, 119° 15′W or 3°20′N, 110°44′W, June 11 or 24, 1970. Perrin field no. WFP80; U.S. National Museum 396174 (complete skeleton). Photographed after frozen for several months and thawed in water.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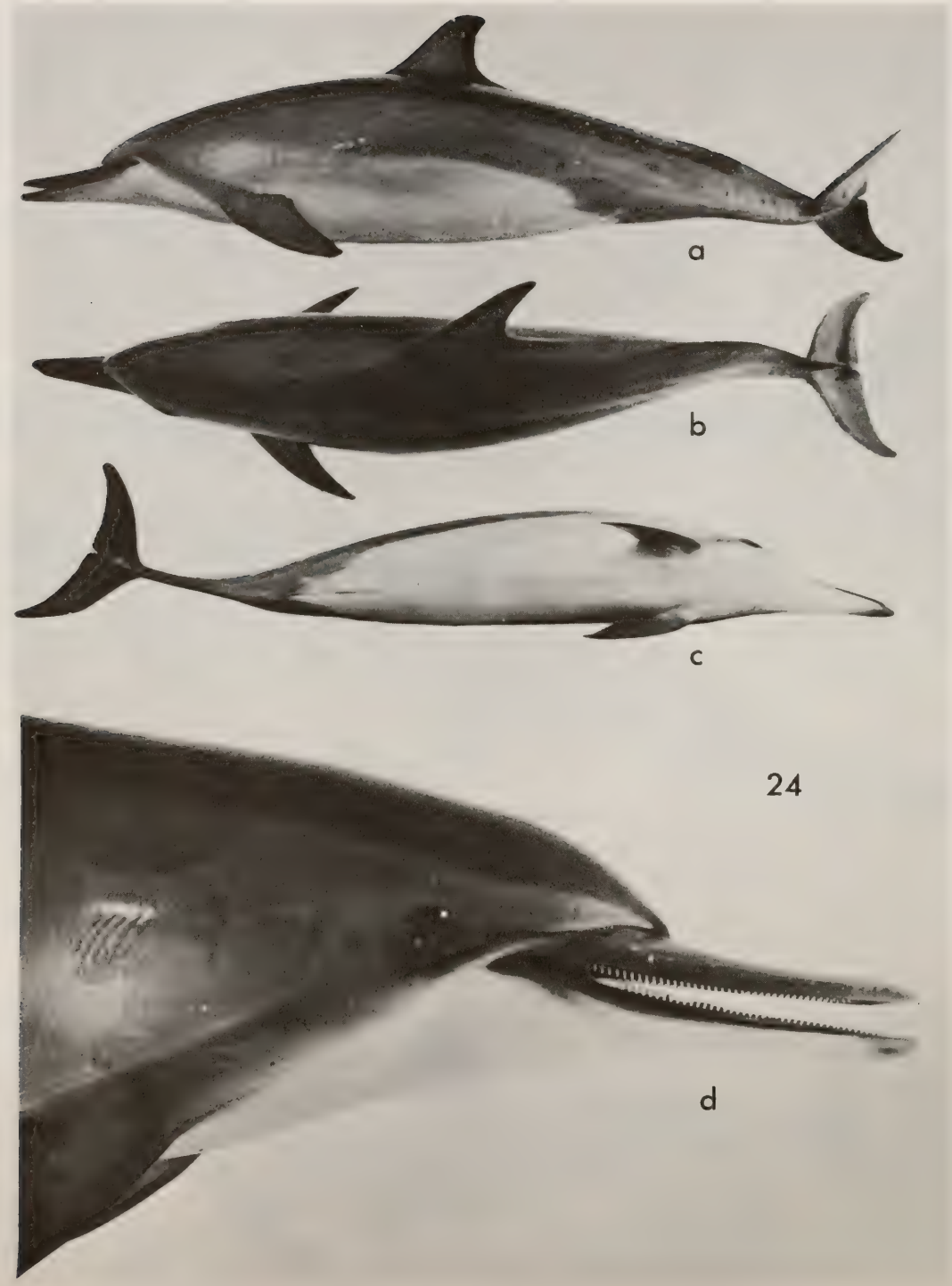
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FIGURE 24.—Lateral (a), dorsal (b), ventral (c), and close-up lateral (d) views of Hawaiian spinner porpoise. Subadult male, 179 cm, from Waikiki Beach, Oahu, May 25, 1970. Oceanic Institute field no. OI70-35; specimen stolen during preparation. Photographed 3 hours after death.

FIGURE 25.—Fetus of eastern spinner. Male, 361 mm, 640 gm, from 9°19′N, 105°20′W, November 10, 1971. Perrin field no. (of mother) WFP187. Specimen at the National Marine Fisheries Service Laboratory, La Jolla, Calif. Photographed underwater after removal from frozen adult, which had been frozen for several months and thawed in water. Dorsal fin folded, and epidermis damaged about head (white areas).

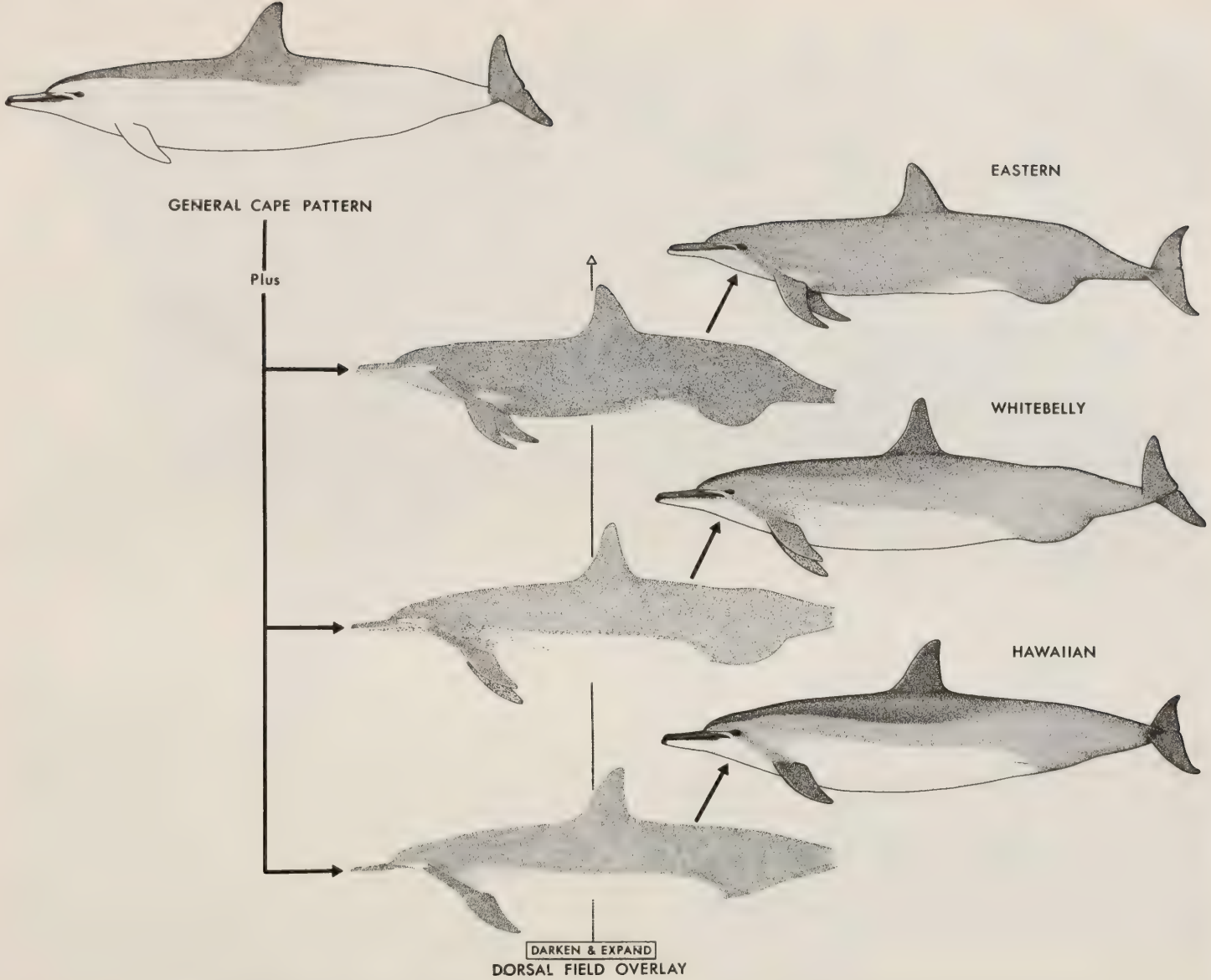

FIGURE 26.—Scheme for analysis of color patterns of spinner porpoises in terms of discrete component systems.

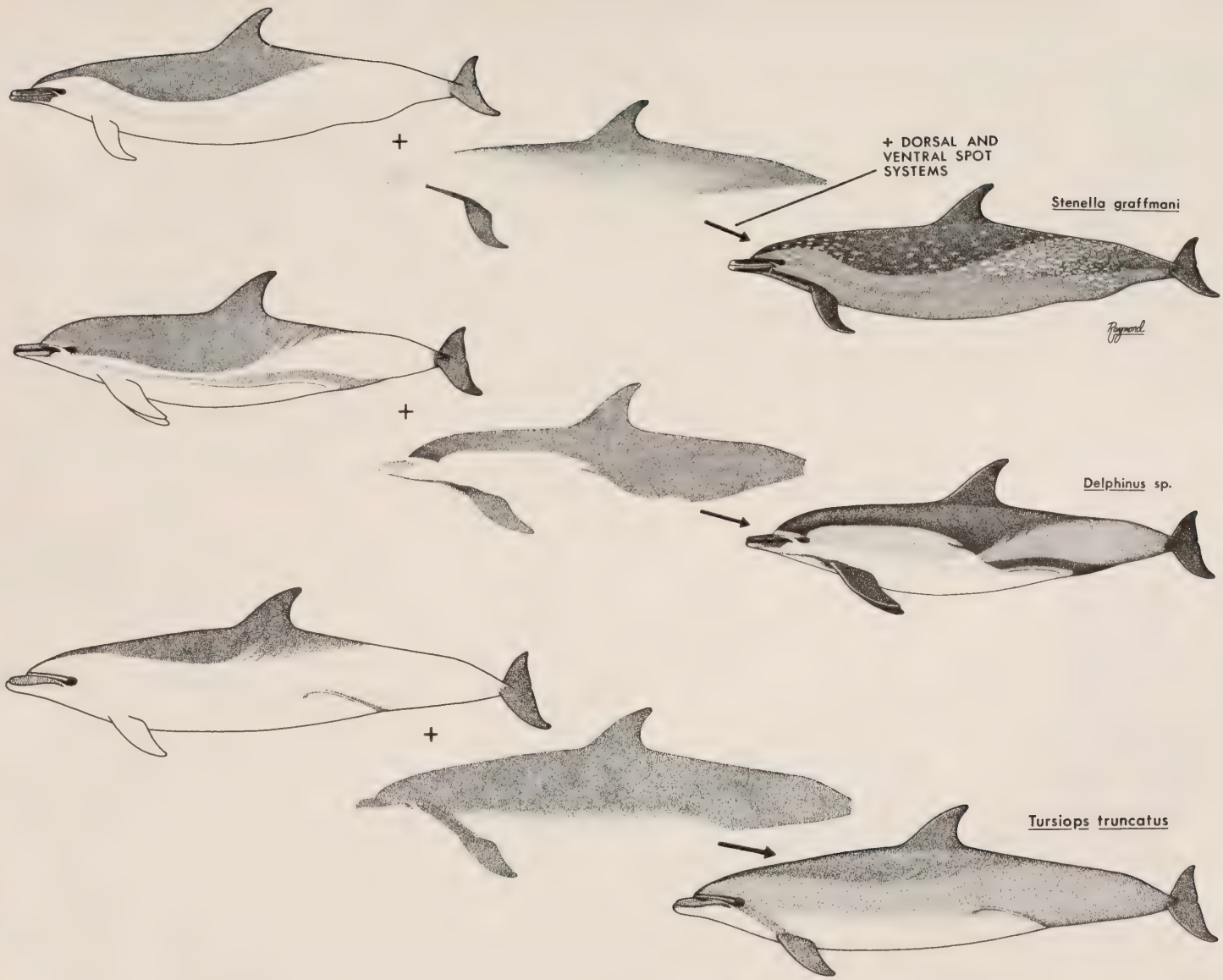

FIGURE 27.—Component analyses of color patterns of *Stenella graffmani, Delphinus* sp. (based on observations of specimens taken off southern California), and *Tursiops truncatus* (based on observations of captive specimens from southeast Atlantic coast of United States).

APPARENT ABUNDANCE OF SOME PELAGIC MARINE FISHES OFF THE SOUTHERN AND CENTRAL CALIFORNIA COAST AS SURVEYED BY AN AIRBORNE MONITORING PROGRAM

JAMES L. SQUIRE, JR.[1]

ABSTRACT

From September 1962 through December 1969, commercial aerial fish spotter pilots estimated tonnage of species observed during flights off the southern and central California coast. Observations of fish and the aircraft's flight route were recorded on special charts. These data were analyzed using 10-minute-longitude by 10-minute-latitude "block areas." A total of over 17,593 flight hours was involved, surveying 57,628 block areas—37,186 during the day and 20,442 during the night. Data from each block area were used to compute diurnal and nocturnal variation in apparent abundance and an annual index of apparent abundance.

Pacific bonito, *Sarda chiliensis*, and yellowtail, *Seriola dorsalis*, were observed in greater frequency and quantity during the day, and the northern anchovy, *Engraulis mordax;* jack mackerel, *Trachurus symmetricus*; and Pacific mackerel, *Scomber japonicus*, were observed in greater frequency and quantity during the night. Pacific barracuda, *Sphyraena argentea*, was observed in greater quantity at night but more frequently during the day.

Between 1963 and 1969 indexes of apparent abundance declined for jack mackerel, Pacific mackerel, Pacific sardine, Pacific bonito, Pacific barracuda, and yellowtail and increased slightly for the northern anchovy. The index closely follows estimates of total abundance for the Pacific mackerel, a species for which reliable estimates of total abundance are available. From observations of the catch trends in the bonito fishery, the index appears to be little affected by changes in economic demand. Its trends in apparent abundance are evident before they are reflected in catches and are useful in the evaluation of catch variations in underutilized resources.

In a search for more efficient fishing methods, many of the fisheries throughout the world that catch pelagic surface schooling species are using aircraft to locate and guide the fleet to the schools and in some cases to direct the catching operation (Cushing, Devold, Marr, and Kristjonsson, 1952). In some areas of the United States the services of the fish spotter are vital to the success of the commercial fleet which depends in part on the aircraft scouting the fishing grounds to obtain current information on the location of near-surface schooling fish (Squire, 1961). At times commercial aerial fish spotters assist the sport fishing fleet by advising them of the location of desirable marine game species.

Data obtainable by techniques of aerial observation have been used by fishery biologists to gain information on distribution and abundance of pelagic near-surface schooling fish.

Sette (1949) investigated the possibilities of aerial scouting for sardines off southern California in search of a method that would provide information useful in estimating abundance yet be free of the availability influence. Aerial scouting was conducted during the day, and commercial fishing was conducted at night. As a result the spotting data were deemed less reliable than those obtained from the commercial fishery.

Jones and Sund (1967), using commercial fish

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spotter aircraft in a search for tuna schools in the same area surveyed by a research vessel, found that the aircraft was about two and one half times more efficient than the vessel at locating fish schools. An evaluation of aircraft by the U.S. Navy, for making biological observations, indicated that for whales the frequency of sighting averaged about 20 times greater than that from ships (Levenson, 1968).

From 1956 to 1964 the California Department of Fish and Game conducted monthly survey flights along the California coast from San Francisco to Mexico. Data were published as flight reports in chart form showing the aircraft's flight track, areas surveyed, notes on species observed, and number of schools and their geographical location. Large variations in the number of schools visible over a short-time period appeared to limit the usefulness of the data, and the surveys were discontinued in 1964. The average number of schools sighted per flight was determined by Wood (1964),[3] and from these data a comparison was made of the relative abundance of northern anchovy, *Engraulis mordax*, schools for the period 1956 through 1963. Limitations on flights to nearshore areas during daylight and low search time in any one area restricted the potential of these surveys for determining the apparent abundance of the many pelagic species found off the California coast.

Fish spotter aircraft range over a large geographical area, and during these flights they may observe concentrations of several species of pelagic fish. Many times these fish are not caught for one or more reasons, such as fishing boats not equipped with proper nets, concentrations are small, species is not economically desirable, and fishing boats are not capable of reaching fish within a reasonable length of time. However, the fish spotters are able to identify these concentrations of fish.

Species commonly observed by the aerial fish spotters within the survey area were northern anchovy, jack mackerel, *Trachurus symmetricus;* Pacific bonito, *Sarda chiliensis;* Pacific mackerel, *Scomber japonicus;* Pacific sardine, *Sardinops sagax*; bluefin tuna, *Thunnus thynnus*; Pacific barracuda, *Sphyraena argentea*; white seabass, *Cynoscion nobilis*; and yellowtail, *Seriola dorsalis.*

The majority of fish spotting effort is directed toward the location and catching of jack mackerel, Pacific mackerel, Pacific bonito, Pacific sardine, and in recent years the northern anchovy. Of these five species the Pacific sardine and Pacific mackerel are most economically desirable with jack mackerel, Pacific bonito, and northern anchovy of descending importance.

To increase knowledge on the apparent abundance of pelagic near-surface marine life, the Tiburon Marine Laboratory initiated a pelagic fish monitoring program in cooperation with aerial fish spotter pilots who are active in spotting for the southern and central California coastal commercial fishery. These cooperators were individuals with specialized training and experience. When assisting the commercial fleet, fishing success is dependent upon accurate identification of schooling species by the spotters. They have considerable experience in estimating the weight of fish schools, and they are considered to be quite accurate in the estimation of weight.

There are a number of variables that affect the statistical accuracy of fish spotter data which are difficult to evaluate, such as individual difference in ability of pilots to locate fish, determine species, and estimate school size, and estimate total tonnage available in a fishing area. Variation in estimating school size probably has more effect on the data than the other variables. However, since at least five experienced observers were used in the program during each year, it was assumed that reasonable annual averages were obtained.

This report consists of an analysis of aerial fish spotter data for the period September 1962 through December 1969 to determine if, for the species commonly observed, it can be used to: (1) compute an accurate index of apparent abundance and (2) obtain a trend in the apparent abundance of pelagic near-surface species and in particular those of underutilized resources.

[3] Wood, R. 1964. Aerial surveys along the California coastline 1956 to 1963. Document V prepared for the Marine Research Committee meeting, March 6, 1964, San Pedro, Calif., 2 p. [Processed.]

METHODS AND PROCEDURES

Five fish spotter pilots were contracted to record observations of pelagic species, giving location, number of schools, estimated tonnage of each school or groups of schools, counts of large marine animals, and flight track for each survey flight. Two pilots usually covered the Santa Barbara Channel and Santa Barbara Islands north to Estero Bay and occasionally into Monterey Bay. The remaining three spotter pilots normally surveyed the area from west of Los Angeles to southwest of San Diego and occasionally offshore to San Clemente Island, Cortez Bank, and San Nicholas Island. Flight operations were conducted during daylight hours or on nights during the dark phase of the moon at elevations of 500 to 1,200 ft (152 to 365 m) above the sea surface.

TECHNIQUES OF OPERATION

Specific observation of a fish school has three phases: (1) distinguishing a school, (2) identifying the species, and (3) estimating weight of the school. The detection of near-surface schools during the day is dependent upon the pilot's ability to distinguish subtle color and light intensity differences in the water. Detection of schools at night is possible only during the dark period of the moon and depends on the pilot's ability to discern gradation of light intensity. Bioluminescence of planktonic organisms agitated by schooling fish indicates by a dull glow the location and size of the school. Species are identified during the day on the basis of a combination of two or more of the following characteristics: color of school or individual fish, shape of school, and behavior and size of individuals within the school. At night, species identification is based on shape of the luminous area and behavior of the schooling fish under undisturbed conditions, or by the behavior of the school after being subjected to a stimulus from an external source such as a flash from the aircraft's landing light.

At first observations were recorded by the pilots on small portable tape recorders. This method was unsatisfactory, and recorders were replaced with three charts covering the coastal waters from the Coronado Islands, Mexico, north to Half Moon Bay, Calif. The charts were completed by the pilots after each flight and were submitted quarterly to the National Marine Fisheries Service. Figure 1 illustrates the type of information recorded by the fish spotter pilot.

PROCESSING OF OBSERVATION DATA

Each chart was overlayed with a 10-minute-longitude by 10-minute-latitude grid, numbered according to the California Department of Fish and Game "Block area" statistical system (Clark, 1935). With the gridded chart, the observation and flight track data could be conveniently tabulated and coded for subsequent computer analysis. California Department of Fish and Game statistical code numbers were assigned to each of the 27 species of marine animals observed. The computer output grouped data by species, year, week, block area, day or night observation, number of schools, tons per school, and tons per block area. The data for block areas were later combined into 11 larger grouped block areas or "zones" lettered A through K (Figures 2 and 3). These zones were selected to outline important geographical areas where fish were commonly observed.

The following criteria were used in tabulating the data from the flight charts:

1. Groups of schools which were indicated on the flight chart as covering more than one block area were listed for each block holding part of the group. For example, if one group of schools (10 schools, 15 tons per school, total 150 tons) overlapped two block areas equally, each area was credited with having 5 schools at 15 tons per school, equalling 75 tons per block area.

2. If only one school was shown overlapping two block areas, the school was assigned to the block area having the greatest portion of the school.

3. If a large area of fish was indicated involving more than two block areas and only a total tonnage estimate made, the tonnage was credited to the block areas in proportion to area outlined.

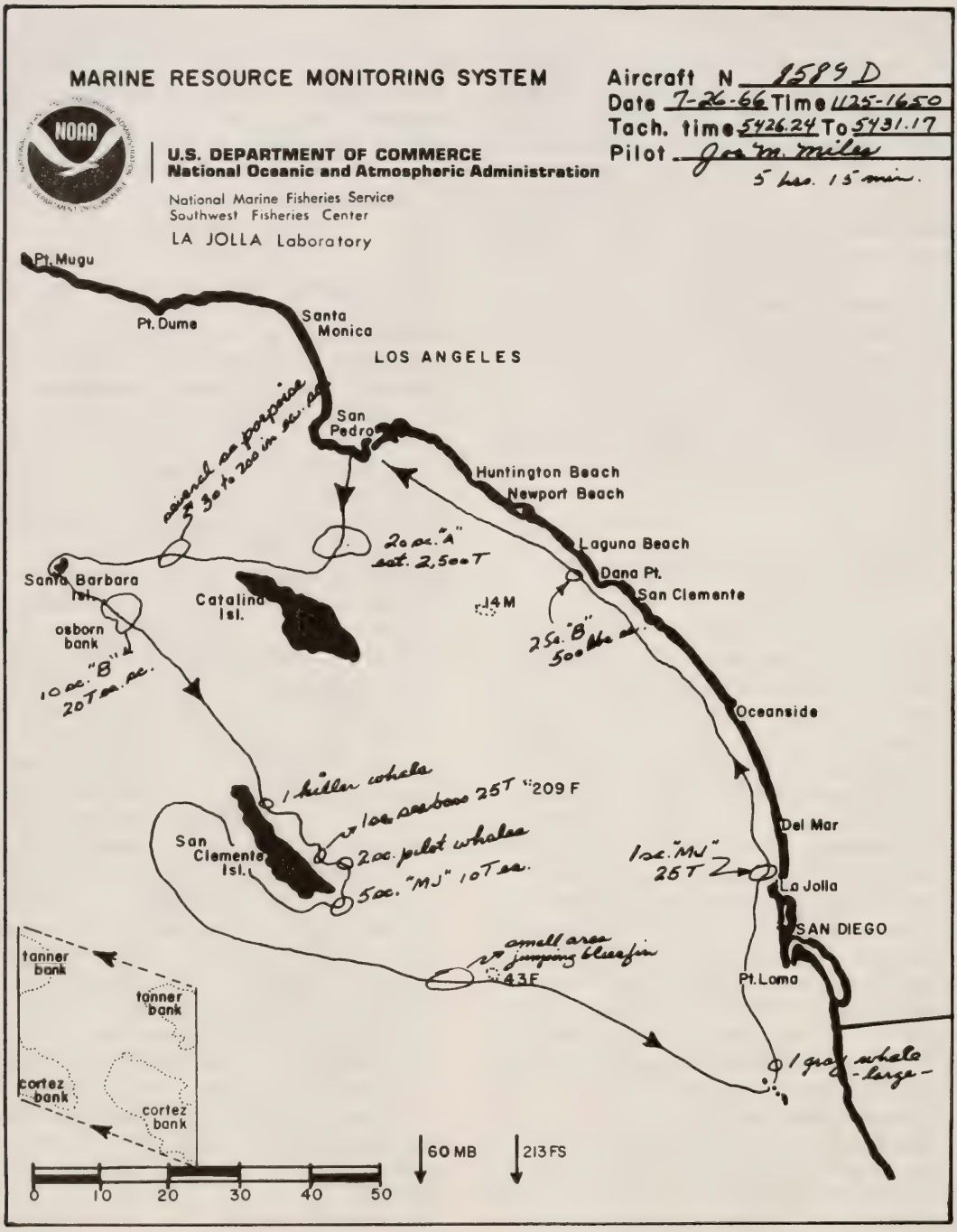

FIGURE 1.—Flight chart for southern California area showing typical flight track and fish and mammal observations. Block area grid is overlayed on chart for coding observations.

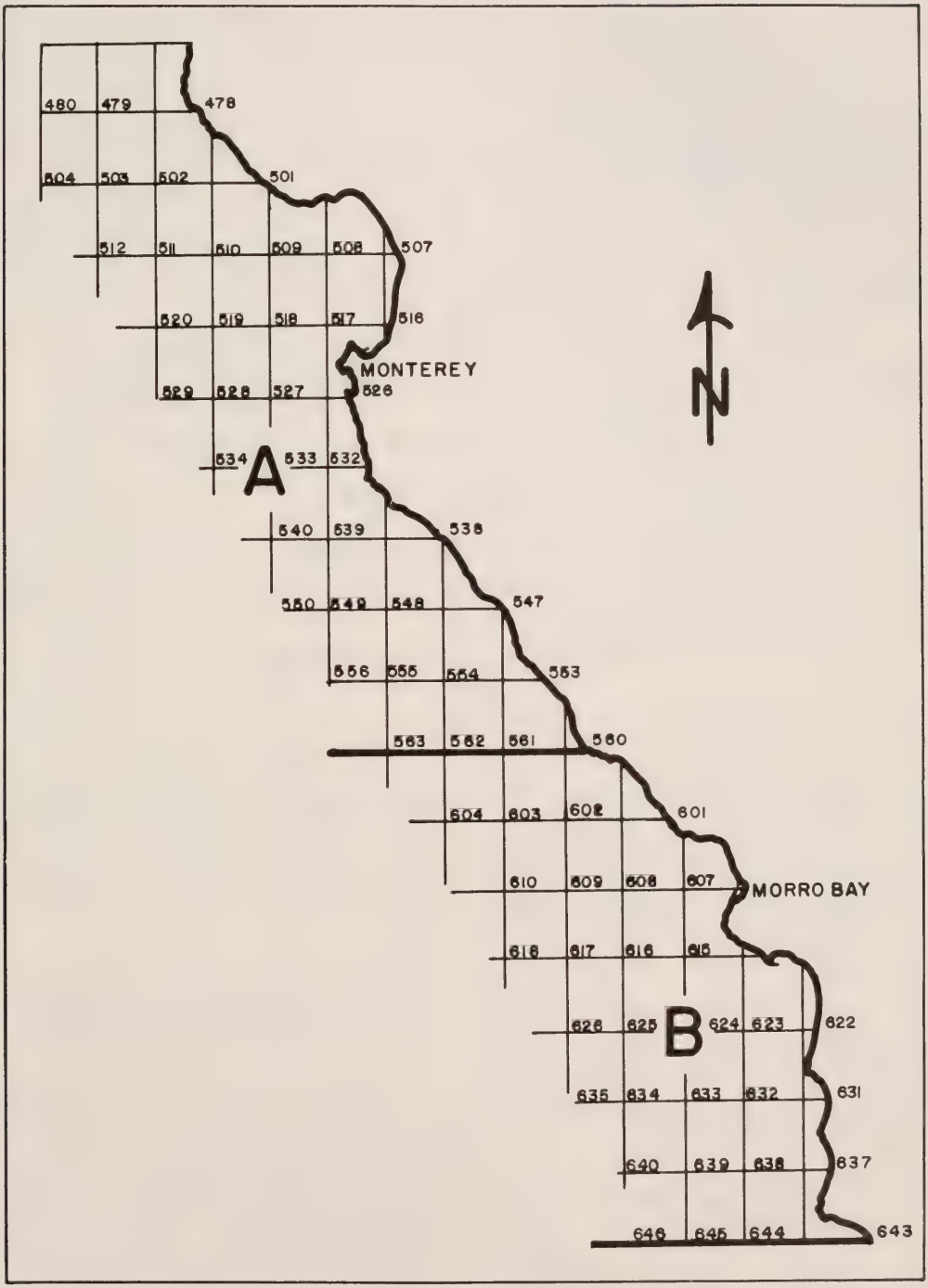

FIGURE 2.—Block areas grouped into zones (A-B), selected to outline the more important coastal fishing areas.

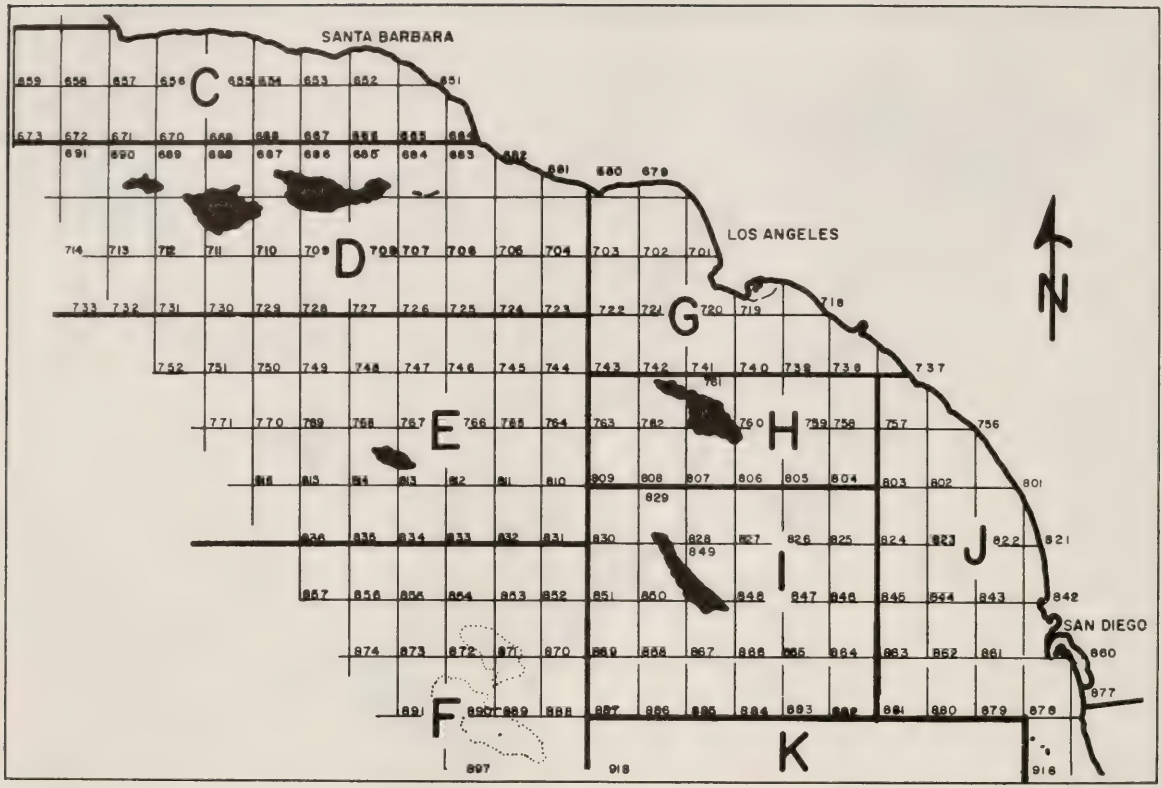

FIGURE 3.—Block areas grouped in zones (C-K), selected to outline the more important coastal fishing areas.

4. Whales, porpoises, and sharks were recorded as numbers of individuals observed.

5. When the flight track entered any portion of a block area, the block area was credited for the purpose of determining observation effort as having a "block area flight."

RESULTS

During survey flights, 20 species of fish were observed and identified. A number of other marine species (mammals, invertebrates) were observed and all are listed in Table 1.

DISTRIBUTION OF FLIGHT OBSERVATION EFFORT

A total of 17,593 flight hours were logged by spotter pilots during the survey period. The number of block area flights from September 1962 through the end of 1969 totaled 57,628 with 37,186 block areas surveyed during the day and 20,442 at night. Distribution of day and night block area flights by year and by zone is shown in Table 2.

NOCTURNAL AND DIURNAL VARIATION IN NUMBER OF SIGHTINGS AND TONNAGE

To determine criteria concerning the frequency of observation during the day and night for each of the species more commonly observed, the ratios in numbers of sightings and tonnages observed were calculated for the period September 1962 through December 1966. Information on the diurnal and nocturnal frequencies and magnitude of occurrence for each species is of importance in evaluating which observation (day

TABLE 1.—Species of fish and other marine animals observed during surveys.

Fish:
- Basking shark *(Cetorhinus maximus)*
- White shark *(Carcharodon carcharias)*
- Northern anchovy *(Engraulis mordax)*
- Pacific sardine *(Sardinops sagax)*
- Pacific bonito *(Sarda chiliensis)*
- Jack mackerel *(Trachurus symmetricus)*
- Pacific mackerel *(Scomber japonicus)*
- Pacific barracuda *(Sphyraena argentea)*
- Yellowtail *(Seriola dorsalis)*
- White seabass *(Cynoscion nobilis)*
- Bluefin tuna *(Thunnus thynnus)*
- Albacore tuna *(Thunnus alalunga)*
- Yellowfin tuna *(Thunnus albacares)*
- Skipjack tuna *(Katsuwonus pelamis)*
- Jacksmelt *(Atherinopsis californiensis)*
- Ocean sunfish *(Mola mola)*
- Striped bass *(Morone saxatilis)*
- Pacific saury *(Cololabis saira)*
- Swordfish *(Xiphias gladius)*
- Striped marlin *(Tetrapturus audax)*

Mammals:
- Gray whale
- Pilot whale
- Blackfish (killer whale)
- Porpoise and dolphin
- Seals and sea lions

Invertebrates:
- Squid
- Jellyfish

or night) might be the more significant in evaluating the trend of apparent abundance. These data were calculated during an earlier part of the study (1962-1966) to evaluate the method of using aerial fish spotter data.

The total amount of fish estimated to have been seen by the aerial fish spotters during the period 1962-1966 was 5,289,521 tons of the following species: northern anchovy, 4,550,218 tons; jack mackerel, 335,794 tons; Pacific bonito, 238,247 tons; Pacific mackerel, 103,464 tons; and yellowtail, 1,955 tons.

Annual sightings of each species per block area flight were expressed as a percentage of all block area flights day and night (% day/% night) and are shown in Table 3. The ratio of diurnal and nocturnal sightings was obtained by dividing the percentage of day sightings by the percentage of night sightings. Ratio values greater than 1.00 indicate a greater number of sightings during day, less than 1.00 indicate greater number of sightings during the night.

To determine the day and night differences in the tonnage observed for each species, the

TABLE 2.—Observation effort (day/night) in block area flights by zone for the period September 1962 through 1969. [Data are presented in number of block area flights (day/night).]

Zone	1962	1963	1964	1965	1966	1967	1968	1969	Total
A	41/62	175/78	125/86	102/84	239/9	361/0	585/0	86/29	1,714/348
B	174/117	220/75	283/156	471/252	770/90	610/13	519/0	126/10	3,173/713
C	104/126	470/658	632/680	892/743	1,860/495	1,016/559	1,014/281	2,130/718	8,118/4,260
D	12/71	137/167	409/518	485/434	1,268/385	813/533	1,000/291	1,942/712	6,066/3,111
E	0/10	63/96	40/263	48/58	108/30	40/51	101/109	87/97	493/714
F	0/6	15/32	23/37	2/106	37/21	15/53	35/194	79/48	206/497
G	0/2	454/496	394/610	481/404	1,358/434	874/596	616/676	735/1,500	4,939/4,718
H	0/0	291/282	363/336	387/349	723/206	435/305	368/469	303/576	2,870/2,523
I	0/0	366/155	477/157	395/258	814/208	614/281	544/378	613/348	3,823/1,785
J	0/0	463/198	586/300	550/128	847/113	1,087/154	672/294	932/188	5,137/1,375
K	0/0	18/0	13/0	13/0	69/9	65/10	75/32	106/1	350/52
Total	331/394	2,672/2,237	3,336/3,143	3,826/2,816	8,120/2,000	5,936/2,555	5,826/3,070	7,139/4,227	37,186/20,442
Grand total	725	4,909	6,479	6,642	10,120	8,491	8,896	11,366	57,628

TABLE 3.—Annual sightings per block area flight in percentage (day/night) and day/night averages and ratios.

Species	1962	1963	1964	1965	1966	Day/night	
						Average	Ratio
Northern anchovy	3.3/21.6	8.7/19.7	7.8/21.5	4.9/11.8	5.4/25.0	6.0/19.9	0.30
Pacific bonito	6.3/ 6.3	7.3/ 5.1	9.7/ 3.4	8.3/ 1.7	6.3/ 2.5	7.5/ 3.8	1.99
Jack mackerel	0.3/ 1.0	3.5/ 9.9	5.0/ 6.7	3.3/ 6.2	1.8/ 5.7	2.7/ 6.1	0.47
Pacific mackerel	0.0/ 6.9	4.2/ 9.6	2.0/ 3.5	0.3/ 1.2	0.1/ 2.0	1.3/ 4.6	0.28
Pacific sardine	1.2/ 1.5	1.5/ 2.3	0.8/ 2.1	0.1/ 0.4	0.2/ 0.4	0.7/ 1.3	0.57
Yellowtail	0.0/ 0.0	1.0/ 0.4	0.2/ 0.0	0.2/ 0.0	0.2/ 0.0	0.3/ 0.0	4.00
Pacific barracuda	1.8/ 0.0	0.9/ 0.6	0.5/ 0.6	0.7/ 0.0	0.2/ 0.1	0.8/ 0.2	3.15

amount observed (day or night) in each zone was divided by the number of block area flights (day or night) within the zone. The average number of tons observed per block area flight for each zone, the average number of tons observed for all zones combined, and ratios of day and night tonnages observed are shown in Table 4. Ratios were obtained by dividing the tons per block area flight (day) by tons per block area flight (night). Therefore, ratios greater than 1.00 indicate greater tonnage during the day, less than 1.00 indicate greater tonnage during the night.

AVERAGE WEIGHT OF FISH SCHOOLS

Average weight of schools was computed for the period September 1962 through December 1966 from all data having estimates of individual schools by weight. As previously indicated, some tonnages were given by areas, not by numbers of schools and tonnages of each school. The average tonnage per school is listed for each species in Table 5.

INDEX OF ANNUAL APPARENT ABUNDANCE

An index of annual apparent abundance was calculated for observations during day and night for each zone and for all zones combined from September 1962 through December 1969 for the northern anchovy, Pacific bonito, jack mackerel, Pacific mackerel, Pacific sardine, yellowtail, and Pacific barracuda. Marr (1951) defined the term apparent abundance as "abundance as affected by availability, or the absolute number of fish accessible to a fishery." This definition of apparent abundance most nearly describes the type of index calculated in this paper.

For convenience in calculating this index, four arbitrary tonnage ranges were selected for each species. Tonnage ranges for each species were selected to cover the entire range of observed tonnages that may occur in any one block area. The midpoint tonnage of each range was divided by 100 for the northern anchovy and by 10 for Pacific bonito, jack mackerel, Pacific mackerel, and Pacific sardine to provide a tonnage range value (X) of convenient size to be used in the

TABLE 4.—Day/night differences in tonnage and ratios observed based on average tons observed per block area flight in each zone for the period September 1962-1966.

Species and zone	Tons/block area flight day/night	Day/night ratio
Northern anchovy		
Zone A	478.8/636.1	0.75
B	148.5/832.2	0.17
C	45.4/386.4	0.11
D	32.6/337.5	0.09
E	9.8/214.0	0.04
F	3.9/ 39.2	0.01
G	105.0/197.3	0.53
H	64.4/ 75.8	0.84
I	10.8/ 92.3	0.11
J	32.6/237.1	0.13
K	13.5/ 11.1	1.21
Average—all zones	79.8/299.7	0.26
Pacific bonito		
Zone A	0.6/ 0.0	--
B	0.5/ 0.2	2.50
C	15.8/ 7.6	2.00
D	12.8/ 2.1	6.09
E	44.5/ 0.1	445.00
F	0.6/ 0.0	--
G	5.8/ 0.9	6.44
H	5.5/ 2.2	2.50
I	7.0/ 0.8	8.75
J	27.6/ 11.3	2.44
K	0.2/ 0.0	--
Average—all zones	10.9/ 2.3	4.73
Jack mackerel		
Zone A	41.7/ 12.2	3.48
B	25.3/ 44.8	0.56
C	2.5/ 6.0	0.41
D	9.2/ 34.6	0.27
E	2.5/ 19.2	0.13
F	8.0/169.4	0.04
G	2.3/ 6.1	0.37
H	1.7/ 8.2	0.20
I	5.8/ 17.0	0.34
J	4.0/ 11.5	0.34
K	0.0/ 0.0	--
Average—all zones	7.7/ 18.4	0.41
Pacific mackerel		
Zone A	0.0/ 0.0	--
B	0.0/ 1.1	0.00
C	0.8/ 5.7	0.14
D	2.5/ 3.8	0.65
E	0.5/ 6.4	0.07
F	50.1/ 50.3	0.99
G	2.0/ 2.0	1.00
H	11.1/ 5.9	1.88
I	1.7/ 2.4	0.70
J	2.7/ 8.4	0.32
K	3.2/ 0.0	--
Average—all zones	2.6/ 5.2	0.50
Pacific sardine		
Zone A	9.5/ 4.5	2.11
B	0.6/ 3.9	0.15
C	0.1/ 0.1	1.00
D	0.2/ 0.2	1.00
E	3.0/ 57.4	0.05
F	16.6/ 6.1	2.72
G	0.2/ 1.2	0.16
H	0.2/ 7.0	0.02
I	0.0/ 0.0	--
J	0.1/ 1.1	0.90
K	0.0/ 0.0	--
Average—all zones	0.7/ 4.1	0.17
Yellowtail	(Note, small number of observations, zone data omitted.)	
Average—all zones	0.09/0.02	4.50
Pacific barracuda	(Note, small number of observations, zone data omitted.)	
Average—all zones	0.06/0.29	0.20

TABLE 5.—Average weight per school (data from September 1962 through December 1966).

Species	Total tons / No. schools obs.	=	Avg. tons/school
Northern anchovy	192,047.5 / 5,261	=	36.5
Pacific sardine	5,140.5 / 194	=	26.5
Jack mackerel	44,545 / 1,846	=	24.1
Skipjack tuna	260 / 14	=	18.6
Albacore	73 / 4	=	18.2
Bluefin tuna	7,092 / 396	=	17.9
Pacific bonito	38,435 / 2,244	=	17.1
Pacific mackerel	10,948 / 649	=	16.9
Yellowtail	754.5 / 53	=	14.2
White seabass	234 / 47	=	4.9
Pacific barracuda	834.5 / 184	=	4.5

index formula. Midpoints were not reduced for Pacific barracuda and yellowtail. Range of observed tonnage and X values are shown in Table 6.

The following formula was used to calculate annual indexes of apparent abundance, day and night, for each species by zone and the day/night index of annual average apparent abundance for each species.

Index of apparent abundance

$$= \frac{\sum N_1X_1 + N_2X_2 + N_3X_3 + N_4X_4}{N_t}$$

where: $N_{1,2,3,4}$ = number of block area flights in which the species occurred at value $X_{1,2,3,4}$.
$X_{1,2,3,4}$ = tonnage range values.
N_t = total number of block area flights in the zone during the year.

Day and night indexes of apparent abundance for each zone and the annual average day/night indexes of apparent abundance for all zones are listed in Table 7.

DISCUSSION AND SUMMARY

A direct, precise measure of total abundance is most desirable for the management of pelagic marine species. However, at the present time and into the foreseeable future, this degree of accuracy in the measurement of total abundance cannot be attained. Therefore, pelagic resource mangement will be required to rely on an indirect measure of total abundance. Some observations on the relation between the index of apparent abundance and changes in estimates of total abundance can be made. For the years 1963 through 1969, either separately or combined, some data are available giving estimates of total abundance, spawning biomass, or indexes of abundance for such species as the northern anchovy, Pacific mackerel, Pacific sardine, jack mackerel, and Pacific bonito. However, all such estimates were calculated from data obtained from such measures as catch, effort, catch composition, fecundity, and egg and larval counts. No direct measurements of total abundance were

TABLE 6.—Range of tonnage and tonnage range values (X).

Species	Observed tonnage	X
Anchovy	0-400	2
	400-1,000	7
	1,000-10,000	55
	10,000-20,000	150
Pacific bonito	0-50	2.5
	50-150	10
	150-1,000	57.5
	1,000-5,000	300
Jack mackerel	0-50	2.5
	50-300	17.5
	300-1,000	65.5
	1,000-2,000	150
Pacific mackerel	0-20	1
	20-100	6
	100-250	17.6
	250-500	37.5
Pacific sardine	0-100	5
	100-500	30
	500-2,000	125
	2,000-4,000	300
Pacific barracuda	0-10	5
	10-30	20
	30-80	55
	80-160	120
Yellowtail	0-5	2.5
	5-10	7.5
	10-30	20
	30-60	45

TABLE 7.—Annual average indexes of apparent abundance for both day and night observations. Dash (__) indicates no flight observations in zone. Indexes given as day/night.

Zone	1962	1963	1964	1965	1966	1967	1968	1969
				Northern anchovy				
A	0.51/1.22	10.98/13.28	0.80/7.32	2.51/2.48	2.02/ 6.33	1.15/ __	0.28/ __	0.00/ 0.00
B	3.25/3.18	6.17/13.02	4.08/3.08	1.85/5.75	0.29/15.31	0.28/ 0.30	0.73/ __	0.03/ 0.00
C	0.05/0.99	0.40/ 2.70	0.90/2.85	1.82/8.63	0.27/ 2.79	2.91/ 3.03	0.05/ 1.76	0.87/ 1.93
D	0.00/2.97	1.24/10.02	0.23/4.75	0.48/3.67	0.14/ 6.73	0.63/ 5.12	0.05/ 3.24	0.41/ 1.96
E	__/0.00	0.00/ 1.05	0.00/3.14	0.00/0.12	1.09/ 0.23	3.15/ 0.11	0.18/ 0.12	0.32/ 0.67
F	__/0.00	3.66/ 1.71	5.75/0.37	0.00/0.58	0.00/ 2.61	0.00/ 0.00	0.00/ 0.60	0.00/ 0.00
G	__/1.00	0.51/ 1.81	0.54/6.21	1.42/3.23	2.24/ 1.78	2.40/ 8.32	0.55/ 2.11	5.01/ 8.57
H	__/__	0.14/ 0.12	0.38/1.00	0.05/1.90	2.28/ 1.43	5.45/ 1.60	0.65/ 0.58	6.35/ 3.26
I	__/__	0.14/ 0.00	0.05/0.11	0.02/0.34	0.28/ 2.53	2.87/ 0.71	0.18/ 0.21	0.78/ 0.49
J	__/__	0.78/ 0.67	0.85/6.08	0.00/0.00	0.45/ 1.55	0.16/20.16	0.52/ 1.11	0.55/ 3.39
K	__/__	0.00/ __	0.00/__	0.00/__	0.00/ 0.22	0.00/ 0.70	2.44/ 0.06	0.00/ 0.00
Average all zones	1.79/1.99	1.64/ 2.99	1.03/3.90	0.96/4.18	0.84/ 3.62	1.78/ 4.30	0.33/ 1.46	1.30/ 4.35
				Pacific bonito				
A	0.00/0.00	0.00/ 0.00	0.50/0.00	0.00/0.00	0.04/ 0.00	0.07/ __	0.00/ __	0.00/ 0.00
B	0.01/0.00	0.00/ 0.01	0.06/0.01	0.02/0.00	0.43/ 0.00	0.01/ 0.00	0.00/ __	0.00/ 0.00
C	0.62/0.25	3.63/ 1.51	2.40/0.82	2.18/0.40	1.38/ 0.83	0.51/ 1.02	0.36/ 1.36	0.29/ 0.27
D	0.83/0.63	0.65/ 1.88	1.40/0.12	0.85/0.10	1.27/ 0.54	0.38/ 0.80	0.53/ 0.15	0.24/ 0.23
E	__/0.00	0.02/ 1.15	0.50/0.00	6.81/0.00	4.30/ 0.00	0.00/ 0.00	0.00/ 0.02	0.00/ 0.00
F	__/0.00	0.00/ 0.00	0.43/0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	__/0.00	0.31/ 0.37	0.30/0.00	0.50/0.01	1.19/ 0.16	0.67/ 0.39	0.12/ 0.13	0.12/ 0.16
H	__/__	0.85/ 0.22	2.12/0.53	2.06/0.32	0.03/ 0.00	0.00/ 0.02	0.68/ 0.24	0.09/ 0.06
I	__/__	0.00/ 0.45	3.46/0.54	0.40/0.13	0.06/ 0.02	0.12/ 0.00	0.02/ 0.03	0.02/ 0.05
J	__/__	3.67/ 0.23	1.10/0.06	1.71/0.46	4.96/ 0.11	3.27/ 0.12	1.70/ 0.69	0.64/ 0.51
K	__/__	0.13/ __	0.00/__	0.00/__	0.00/ 0.00	45.73/ 0.00	0.26/ 0.00	0.75/ 0.00
Average all zones	0.23/0.19	1.62/ 0.58	1.62/0.28	1.26/0.19	1.34/ 0.35	1.35/ 0.34	0.43/ 0.35	0.26/ 0.18
				Jack mackerel				
A	0.00/0.08	1.81/ 0.00	8.32/2.89	0.78/ 1.67	4.29/25.72	0.81/ __	0.91/ __	0.03/ 0.00
B	0.02/0.00	3.48/ 1.37	6.65/6.67	1.03/ 1.22	0.74/ 8.78	0.78/ 1.34	0.70/ __	0.00/ 0.00
C	1.59/0.45	0.96/ 0.49	0.83/0.56	0.14/ 0.33	0.06/ 0.03	0.04/ 0.33	0.13/ 0.02	0.11/ 0.17
D	0.00/1.45	1.79/13.77	2.72/5.36	1.44/ 1.40	0.24/ 1.62	0.41/ 0.24	0.21/ 0.20	0.15/ 0.33
E	__/0.00	0.27/ 4.74	0.93/2.31	0.72/ 1.55	0.16/ 7.38	0.00/ 2.15	0.24/ 4.09	0.00/ 4.41
F	__/2.91	11.16/39.70	1.63/2.31	0.00/17.41	0.00/27.91	0.00/38.84	10.87/27.77	3.50/13.08
G	__/0.00	1.23/ 1.76	0.64/0.99	0.02/ 0.29	0.00/ 1.05	0.00/ 0.10	0.02/ 0.00	0.13/ 0.26
H	__/__	0.56/ 1.34	0.01/1.11	0.71/ 0.43	0.04/ 2.18	0.01/ 0.33	0.00/ 0.26	0.00/ 0.59
I	__/__	2.11/ 5.53	0.17/1.86	1.35/ 0.75	0.19/ 2.37	0.04/ 3.27	0.00/ 1.27	0.04/ 1.58
J	__/__	0.67/ 0.54	0.72/1.51	0.86/ 0.96	0.00/ 0.06	0.00/ 0.03	0.08/ 1.07	0.06/ 0.30
K	__/__	0.00/ __	0.00/__	0.00/ __	0.00/ 0.00	0.00/ 1.75	0.00/ 1.09	0.00/ 0.00
Average all zones	0.51/0.46	1.41/ 2.98	1.62/2.18	0.71/ 1.36	0.28/ 1.94	0.20/ 1.41	0.30/ 2.25	0.11/ 0.65
				Pacific mackerel				
A	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ __	0.00/ __	0.00/ 0.00
B	0.30/ 0.03	0.00/ 1.56	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ __	0.00/ 0.00
C	0.00/ 3.15	0.23/ 0.37	0.03/0.30	0.04/ 0.28	0.01/ 0.35	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
D	0.50/ 0.30	1.41/ 2.20	0.49/0.23	0.05/ 0.08	0.00/ 0.01	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	__/ 3.75	0.43/ 0.67	0.02/0.74	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.03	0.00/ 0.00
F	__/ 0.00	5.40/ 6.59	3.15/3.62	0.00/ 0.23	0.00/ 2.95	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	__/18.75	0.79/ 0.46	0.78/0.13	0.00/ 0.44	0.00/ 0.04	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	__/ __	2.19/ 1.62	0.14/0.36	0.00/ 0.02	0.00/ 0.02	0.00/ 0.00	0.00/ 0.00	0.00/ 0.03
I	__/ __	0.76/ 0.40	0.01/0.53	0.00/ 0.11	0.00/ 0.09	0.00/ 0.02	0.00/ 0.00	0.00/ 0.04
J	__/ __	0.83/ 1.44	0.75/0.29	0.00/ 0.36	0.00/ 0.06	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
K	__/ __	1.94/ __	0.00/__	0.00/ __	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.17/ 1.26	0.79/ 0.91	0.33/0.33	0.01/ 0.19	0.00/ 0.14	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00

TABLE 7.—Continued.

Zone	1962	1963	1964	1965	1966	1967	1968	1969
				Pacific sardine				
A	0.00/ 0.00	1.40/ 3.78	1.22/0.05	0.04/ 0.00	0.00/ 0.00	0.00/ --	0.00/ --	0.00/ 0.00
B	0.05/ 2.13	0.31/ 0.00	0.26/1.63	0.00/ 0.00	0.00/ 0.38	0.00/ 0.00	0.00/ --	0.00/ 0.00
C	0.04/ 0.00	0.02/ 0.00	0.00/0.05	0.07/ 0.02	0.00/ 0.00	0.00/ 0.03	0.00/ 0.00	0.00/ 0.00
D	0.00/ 0.28	0.07/ 2.36	0.23/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	--/12.50	2.22/ 0.83	1.75/7.87	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
F	--/ 0.00	0.00/ 0.00	13.47/1.62	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	--/ 0.00	0.08/ 0.30	0.17/0.13	0.03/ 0.00	0.00/ 0.09	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	--/--	0.06/ 0.67	0.00/2.27	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.02	0.00/ 0.00
I	--/--	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.02	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
J	--/--	0.12/ 0.05	0.22/0.01	0.00/ 1.09	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
K	--/--	0.00/ --	0.00/--	0.00/ --	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.04/ 1.00	0.22/ 0.50	0.27/1.03	0.02/ 0.05	0.00/ 0.04	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
				Pacific barracuda				
A	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ --	0.00/ --	0.00/ 0.00
B	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.24/ 0.00	0.00/ 0.00	0.00/ --	0.00/ 0.00
C	0.00/ 0.00	0.34/ 0.43	0.45/0.48	0.25/ 0.00	0.02/ 0.00	0.02/ 0.00	0.03/ 0.01	0.04/ 0.00
D	0.00/ 0.00	0.00/ 0.00	0.00/0.01	0.00/ 0.00	0.01/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
F	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	--/ 0.00	0.00/ 0.11	0.00/0.00	0.02/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	--/ --	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.11/ 0.00	0.00/ 0.00	0.00/ 0.00
I	--/ --	0.00/ 0.00	0.00/0.31	0.40/ 0.00	0.02/ 0.00	0.01/ 0.00	0.00/ 0.00	0.00/ 0.00
J	--/ --	0.15/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.04/ 0.00
K	--/ --	0.04/ --	0.00/--	0.00/ --	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.00/ 0.00	0.08/ 0.15	0.08/0.12	0.10/ 0.00	0.03/ 0.00	0.00/ 0.00	0.01/ 0.00	0.02/ 0.00
				Yellowtail				
A	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ --	0.00/ --	0.00/ 0.00
B	0.00/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.07/ 0.00	0.00/ 0.00	0.00/ --	0.00/ 0.00
C	0.00/ 0.00	0.03/ 0.04	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
D	0.00/ 0.00	0.36/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
E	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
F	--/ 0.00	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
G	--/ 0.00	0.00/ 0.00	0.00/0.00	0.01/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
H	--/ --	0.00/ 0.00	0.00/0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
I	--/ --	0.55/ 0.64	0.13/0.04	0.34/ 0.07	0.39/ 0.00	0.09/ 0.00	0.00/ 0.00	0.00/ 0.00
J	--/ --	0.63/ 0.10	0.00/0.00	0.16/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
K	--/ --	0.00/ --	0.00/--	0.00/ --	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00
Average all zones	0.00/ 0.00	0.19/ 0.06	0.01/0.00	0.06/ 0.00	0.04/ 0.00	0.00/ 0.00	0.00/ 0.00	0.00/ 0.00

made which would provide a precise count of the population size.

From data for 1962 through 1966 the diurnal/nocturnal ratios in tonnage observed and in sightings indicate that the northern anchovy, jack mackerel, Pacific mackerel, and Pacific sardine were observed more frequently and in greater quantities at night. Pacific bonito and yellowtail were observed more frequently and in greater quantities during the day. However, Pacific barracuda were observed in greater quantity at night but more frequently during the day.

Indexes of apparent abundance for day and night observations and variations in total commercial catch (Lyles, 1963, 1964, 1965, 1966; Keilman and Allan, 1969) during the years 1963 through 1969 are shown in Figures 4 through 7. The records for 1962 were incomplete (program initiated in September 1962) and were not considered in the discussion of the index.

In consideration of the day/night ratios, the indexes reflect the following:

Pacific sardine (Figure 4)—The Pacific sardine is observed in greater quantity and more frequently during the night; therefore, the night index should provide a better measure of the sardine's apparent abundance. The night index declined from 0.50 in 1963 to an index of less

than 0.00 in 1969. Some positive index values of less than 0.005 will be recorded as 0.00.

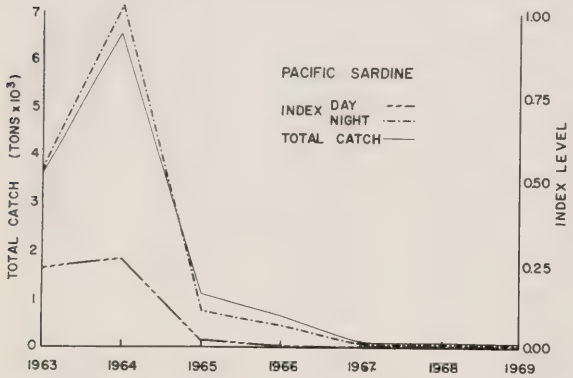

FIGURE 4.—Total catch and average index value for the Pacific sardine.

Pacific mackerel (Figure 5)—Data show that Pacific mackerel are observed in greater frequency and abundance during the night; therefore, the night index should be a better indicator of apparent abundance. The night index declined sharply from 0.91 in 1963 to 0.14 in 1966 and continued the decline to less than 0.00 in 1969.

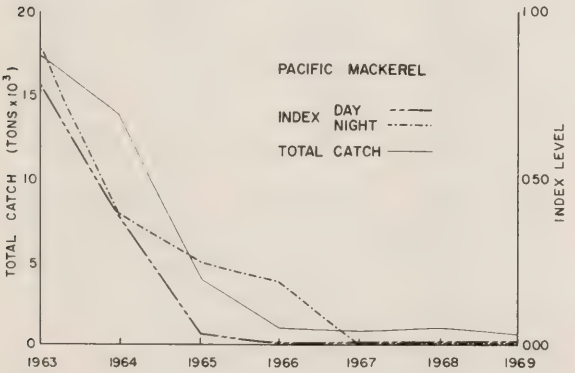

FIGURE 5.—Total catch, average index values for the Pacific mackerel.

Jack mackerel (Figure 6)—Observation of data show that jack mackerel is sighted more frequently and in greater abundance during the night; therefore, the night index should be the best measure of apparent abundance. The night index declined from 2.98 in 1963 to 1.36 in 1965; however, the index level showed an increase in 1968 to 2.25 and a sharp decline in 1969 to 0.65.

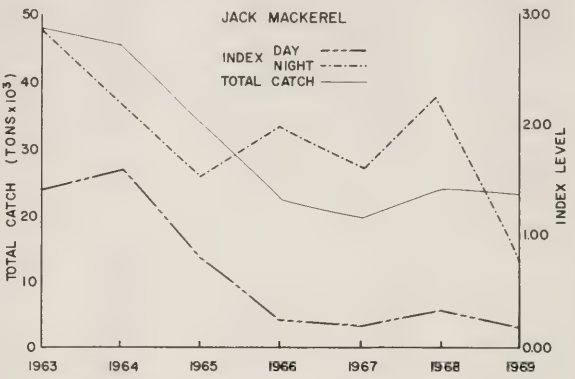

FIGURE 6.—Total catch and average index values for the jack mackerel.

Pacific bonito (Figure 7)—Bonito are observed in greater frequency and abundance during the day; therefore, the day index better represents any changes in apparent abundance. The day index showed only a slight decline during the 1963-1967 period, declining from 1.62 to 1.34. However, since 1967 the index has declined rapidly to a low in 1969 of 0.18.

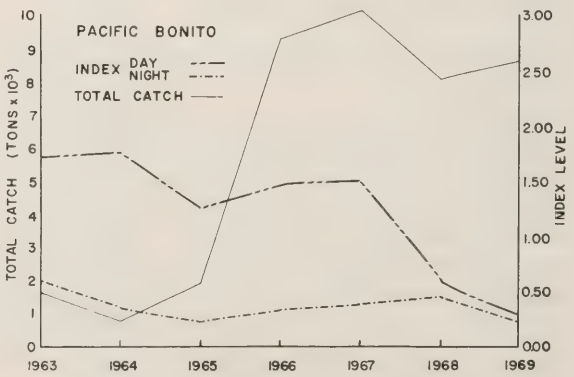

FIGURE 7.—Total catch and average index values for the Pacific bonito.

Northern anchovy (Figure 8)—Data indicate that the northern anchovy is observed more frequently and in abundance during the night; therefore, the night index should better reflect the apparent abundance of this species. The night index increased from 2.99 in 1963 to 4.30 in 1967, declined in 1968 to 1.46, and increased to a high level of 4.35 in 1969.

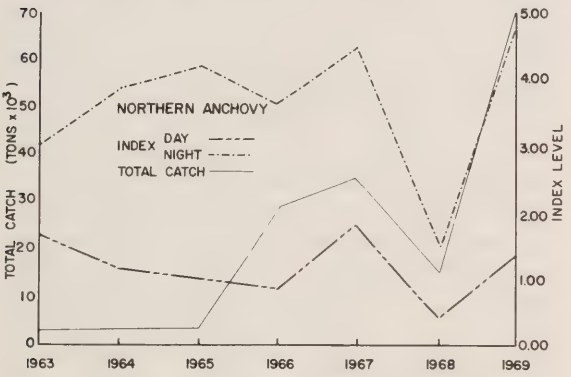

FIGURE 8.—Total catch and average index values for the northern anchovy.

Yellowtail and barracuda—Indexes have declined for both species (see Table 7); however, the frequency of observation was low, and no comparisons can be made with trends in abundance.

The relation between the trend of the apparent abundance index and of the trend of abundance estimates, where available, are discussed for the following species:

Pacific sardine—During the period 1963-1969, the Pacific sardine population continued to decline to a very low level, and the population is now at a fraction of that calculated for the 1930's and 1940's. Since no recent annual estimates are available (latest is 190,000 tons for 1959), a direct comparison of the estimates of total abundance with the index of apparent abundance cannot be made; however, the trend of the index follows closely the downward trend of the commercial catch.

Pacific mackerel—The Pacific mackerel fishery in southern California has been the subject of comprehensive research by the California Department of Fish and Game for many years. For purposes of comparison between trends of the index and population estimates, the more recent data for Pacific mackerel provides the best source of comparative statistics.

The Pacific mackerel catch has declined to a low level in recent years, and the trend of the index follows closely the catch decline (see Figure 5). Population estimates have been calculated by a number of workers. Blunt and Parrish (1969) summarized the knowledge of this fishery and reported estimates of total spawning biomass of 160 million pounds in 1963. Blunt[3] (personal communication) computed revised estimates for California waters using a modification of the Murphy method (Murphy, 1966). Revised figures indicate a spawning biomass of 64.5 thousand tons in 1962 and 78.5 thousand tons in 1963 reducing to less than 5,000 tons in 1968, an 84% or more, decline from 1963. The night index follows this 84% decline in estimated spawning biomass with an 89% index decline from 1.26 in 1963 to 0.14 in 1966 and to less than 0.00 in 1968.

Jack mackerel—Jack mackerel total abundance estimates are derived from egg and larval surveys. Ahlstrom (1968) estimated the adult spawning population in 1951-1954 for the California area to be between 1.4 and 2.4 million tons and that the resource was "much to moderately underutilized." In 1968 he estimated the population level to be approximately the same as was found in the earlier years.

The commercial fishery has experienced a substantial decline in catch over the past years and has extended its fishing grounds further offshore. Ahlstrom (1968) indicated the spawning population is centered in the oceanic waters. Blunt (1969) reported that in this offshore area the population is comprised of mature adults, some reaching the age of 30 years. The young fish remain inshore until 3 to 6 years old and then inhabit the offshore waters where they are outside the range of the normal fishery. The night aerial index shows a decline in apparent abun-

[3] C. E. Blunt, Jr., California Department of Fish and Game, Marine Resources Brancsh, 1416 Ninth St., Sacramento, CA 95814.

dance of these inshore younger fish, and this decline follows the downward catch trend.

Pacific bonito—The Pacific bonito has been abundant in southern California waters since the advent of the "warm years" of 1957-1958. Its northward latitudinal range into southern California waters is influenced by environmental conditions (Radovich, 1963). Figures on total abundance are not available. However, an index of abundance off southern California was developed from party boat catches by Radovich (1963). It is believed that party boat catches reflect the bonito's general abundance off southern California within certain limits. These limits were not defined and are due to the anglers preference for fishing more desirable species such as barracuda, yellowtail, albacore, etc., when they are available rather than fishing for bonito. Blunt (personal communication; see footnote 3) continued Radovich's study and calculated an index based on catch per angler day for the years 1962 through 1968. Values are as follows: 1962, (1.7), 1963 (1.5), 1964 (2.4), 1965 (1.4), 1966 (0.9), 1967 (0.6), 1968 (1.4). The highest party boat index level was in 1964. The index shows an increase for 1968 and differs from the index of apparent abundance; however, this index has shown an overall decrease since 1964.

The day index of apparent abundance shows an overall decrease from 1963 through 1969. The Pacific bonito is classed as "much underutilized" by Ahlstrom (1968). Due to economic factors and a decline in catches of jack and Pacific mackerel, the catch of bonito increased sharply in 1966 and 1967 with only a slight reduction in catch during 1968 and 1969. In contrast to this increase in catch level, the index of apparent abundance has shown a substantial decrease from 1.26 in 1965 to 0.26 in 1969. A considerable reduction in catch was experienced in 1970 (Lester A. Keilman, personal communication) as the total catch declined to 4,600 tons, about one-half the 1969 catch.

Northern anchovy—Studies by Ahlstrom (1968) estimated a total population of 1.8 to 2.3 million tons in 1958, increasing to 4.5 to 5.6 million tons in 1968. This estimate was based on data from larval counts and shows a population increase of approximately 8.6 times during the period 1951 through 1968. No total population estimates for the successive years 1963 through 1969 are available; however, Ahlstrom does state that the larval counts show that the population is somewhat variable from year to year and that the population reached a plateau in about 1962. Since annual abundance estimates are not available for the years 1963 through 1969, a direct comparison with the aerial spotter index cannot be made. The northern anchovy has increased substantially in abundance during the past decade and is classed as an underutilized species (Ahlstrom, 1968). Since it has been subjected only to minor fishery, except in 1969, it is generally agreed that the population level continued to be at high level throughout the years 1963-1969. The trend of the night aerial index of apparent abundance shows an overall increase during the years 1963 through 1969. The only significant change in apparent abundance was in 1968 when the index declined sharply; however, in 1969 it again increased to a high level.

Wide fluctuations in anchovy relative abundance were noted by Wood (1964, see footnote 2) during aerial surveys from 1956 to 1963. Future observations will determine if this paralleling of catch and apparent abundance will continue. Since the survey area covers an area common to the anchovy, trends in the annual index should be of use in evaluating catch variations and reflect the trend of total abundance in this underutilized resource.

In summary, for the geographical area normally surveyed by the aerial fish spotter, the author believes these data represent a reasonable index of apparent abundance. Like all other measures presently available, the true relation of the index of apparent abundance to total abundance for each species cannot be determined. However, from all data available concerning the Pacific mackerel, a species for which considerable and more reliable data on the adult population are available, the trend of the index follows the downward trend of the total abundance estimate. The index shows little effect from fluctuations in economic demand, as shown in data for the Pacific bonito. Trends in the abundance level of the Pacific bonito within the survey area are evident before they are reflected

in catches, and it appears to be a useful index in the evaluation of catch variations and long-term trends in total abundance in underutilized pelagic surface schooling resources.

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The studies of Dr. Oscar E. Sette in the late 1940's must be recognized as one of the earliest applications of scientific aerial fish observations in the continuing search for new methods and techniques for obtaining abundance estimates of pelagic fishery resources.

Reynold A. Fredin of the National Marine Fisheries Service, Northwest Fisheries Center, Seattle, Wash., gave valuable assistance through suggestions on statistical processing methods for the aerial spotter data, as did Norman Abramson[4] of the California Department of Fish and Game, Marine Resource Laboratory, Long Beach, Calif. The processing of the data by the Statistical Section of the California Department of Fish and Game, Marine Resources Laboratory under the direction of Edward Greenhood was appreciated, as were suggestions of the staff of the Statistical Section on original coding of the data.

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AN APPLICATION OF YIELD MODELS TO A CALIFORNIA OCEAN SHRIMP POPULATION

NORMAN J. ABRAMSON[1] AND PATRICK K. TOMLINSON[2]

ABSTRACT

Two types of yield models were utilized to analyze fishery data from California's northernmost bed of ocean shrimp, *Pandalus jordani*. The Schaefer form of stock production model was applied to catch and effort data for the years 1954 through 1969. Age-structured catch data for 1955 through 1968 were analyzed by the Murphy method to obtain mortality rates and biomass estimates. Catchability coefficients and a growth curve were also estimated. Attempts to fit spawner-recruit models to estimates obtained from the age-structured catch data were inconclusive; so, age specific mortality and growth estimates were only used to fit a yield-per-recruit model.

After comparing the results from the two models, the Schaefer model was deemed most suitable for managing this fishery. The model estimated the maximum sustainable yield at 2.46 million pounds. A strategy for managing the fishery under a quota system was proposed.

The fishery for ocean shrimp, *Pandalus jordani*, in California has a unique importance despite the fact that it does not rank high among the State's fisheries in terms of pounds landed or value of the landings. This unique importance exists since the fishery developed after discovery of the shrimp beds by the California Department of Fish and Game's exploratory fishing and because it has been under continuous quota control by the California Fish and Game Commission since the fishery's inception in 1952 (Dahlstrom 1961, 1970). It is also the only California commercial fishery whose catch is fully regulated under a quota system.

This paper is limited to a discussion of the population and fishery which range along the coast from the mouth of the Mad River in California to the Rogue River in Oregon. This fishery consists primarily of regulated California vessels, but there is a small Oregon fleet not covered by California's regulations while fishing north of the California border. Three smaller populations which occur farther south in California are not considered here.

Initially, quotas were set arbitrarily at one-fourth the estimated biomass on the bed. Biomass was originally estimated from an examination of commercial catch data and later from research vessel cruise data. In later years, quota recommendations were at least partially directed toward allowing what was deemed an appropriate spawning stock to remain at the end of the season. Spawning stock values were based on estimated preseason year class abundance and estimated survival over the fishing season.

Estimating procedures which assume commercial or research fishing gear catches all shrimp in the water column above the swept path must inherently be negatively biased since escapement over, around, and through the gear occurs. The methods just discussed are of this type. A more complete account of the basis for quota recommendations prior to 1969 is found in Dahlstrom (1961, 1970), Dahlstrom and Gotshall (1969), and Gotshall (in press).

Over the history of this fishery substantial amounts of data have been collected. Of relevance to this paper are catch and effort data, estimated age and sex composition of landings,

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and research vessel biomass estimates for 1965 through 1968. These data were used in applying a stock production model and a dynamic pool model. The general characteristics of these two models were discussed by Schaefer and Beverton (1963) under the designations of "Schaefer Approach" and "Beverton-Holt Approach," respectively.

STOCK PRODUCTION MODEL

From an operational viewpoint stock production models possess the advantage of requiring only catch and effort data, which are usually available at relatively little expense, for their fitting. Another desirable characteristic is the inclusion of density dependent effects, even though they are treated grossly and population response to density is assumed to be instantaneous. Pella and Tomlinson (1969) discuss the assumptions implicit in the model. The most notable fisheries application of this type model was to yellowfin tuna of the eastern Pacific by Schaefer (1954, 1957), who developed a method for fitting the model to a population in a non-equilibrium state.

Pella (1967) examined a number of methods for estimating parameters of the Schaefer model and concluded that a surface searching technique for minimizing the summed, squared deviations between observed catches and catches predicted by an integrated form of the Schaefer model was generally most satisfactory.

Pella and Tomlinson (1969) generalized the Schaefer model to allow asymmetry in the integrated form and gave the population growth rate as

$$\frac{dP(t)}{dt} = HP^m(t) - KP(t) - qf(t)P(t), \quad (1)$$

where H, K, m, and q are constants. $P(t)$ represents the population size at time t, $f(t)$ is the fishing intensity at t, q is the catchability coefficient, and m determines the amount of asymmetry in the equilibrium yield curve. In the Schaefer model, $m = 2$ and the equilibrium curve is a parabola. The integral of (1) from time 0 to t with f constant is

$$P(t) = \left[\frac{H}{K+qf} - \left(\frac{H}{K+qf} - P(0)^{1-m} \right) \times e^{-(K+qf)(1-m)t} \right]^{\frac{1}{1-m}} \quad (2)$$

and Pella and Tomlinson (1969) used a numerical approximation of

$$C(t) = \int_0^t qf(t)P(t)\,dt \quad (3)$$

for computer calculation of expected catch over the interval. Pella (1967) gives the integrated form of (3) for the Schaefer model.

A computer program, GENPROD, (Pella and Tomlinson, 1969) for fitting the generalized model to catch and effort data uses the criterion of least squares between observed and predicted catches. Fox (1971) discusses least squares for estimating parameters in (2) and suggests alternatives which may be preferable to that used by GENPROD.

CATCH AND EFFORT DATA

Catch and effort data have been collected since the beginning of the fishery in 1952, but data from the first 2 years of the fishery are not used in this study because there was little effort and low catch-per-effort values indicated that fishermen had not fully acquired the skills needed for successfully catching shrimp. California landings were obtained from market receipts, and effort by California vessels was obtained from compulsory logbooks carried by all California trawlers. Oregon landings and effort were supplied by the Oregon Fish Commission (Jack Robinson, Oregon Fish Commission, personal communication).

California vessels were restricted to use of beam trawls until otter trawls became legal in 1963. Oregon vessels have used otter trawls since their entry into the fishery in 1960. A correction factor was used to convert California beam trawl effort to otter trawl effort for 1954 to 1962.

Fishing power of beam trawls relative to otter trawls was estimated from 40 pairs of catch-per-hour statistics. These paired statistics consisted of the average weekly catch-per-hour for

each gear within a 10-fm depth interval bounded by a 10-min by 10-min block area. The data were collected during 1960 through 1962 when Oregon vessels were using otter trawls and California vessels were still restricted to beam trawls. California Department of Fish and Game trawler logbooks and information supplied by the Oregon Fish Commission were the sources of the records (Tom Jow, California Department of Fish and Game, personal communication).

With otter trawl taken as the standard gear, the relative log fishing power of beam trawls was computed by Robson's (1966) method except the two gear types were used in a manner analogous to his treatment of individual vessels. If the logarithm of catch-per-hour is normally distributed and the other assumptions of Robson's model hold, then his method produces B_i, an unbiased estimate of relative log fishing power, β_i, for the ith gear. However, exp (B_i) is a biased estimate of exp (β_i). An unbiased estimator for exp (β_i) is given by Laurent (1963) as

$$\widehat{\exp(\beta_i)} = \left[\exp(B_i)\right]\left[1 + \sum_{j=1}^{\infty} \frac{(-1)^j}{j!2^j} \times \frac{(n-k-1)^j \left[v(B_i)\right]^j}{(n-k-1)(n-k+1)\ldots(n-k+2j-3)}\right], \quad (4)$$

where $v(B_i)$ is an unbiased estimate of the variance of B_i with $n-k-1$ degrees of freedom. Robson's method provides $v(B_i)$ and our computer program for calculating fishing power carries the series expansion in (4) to 15 terms. This computer program is described by Berude and Abramson (1972) and a FORTRAN listing is contained in Abramson (1971).

The estimated fishing power of beam trawls relative to otter trawls in the shrimp fishery was 0.71; all beam trawl effort used in this study was adjusted by that factor.

FITTING THE PRODUCTION MODEL

Usable catch and effort data covered a period of 16 years, each divided into open and closed seasons. Each season was treated as a separate interval in the fitting procedure and thus population estimates were obtained at 32 points in time. Table 1 shows catch, adjusted effort, and time for the series of seasons used to fit the generalized production model.

When initially fitting GENPROD to the data the parameters representing optimum effort (F_{opt}), catchability coefficient (q), maximum catch-per-effort (U_{max}), and the ratio of initial population to maximum population (r) were unrestricted. Pella and Tomlinson (1969) give these parameters as transformations of those in (2). The equation was fitted with the parameter m taking values from 1.4 to 2.6 by increments of 0.2. Results showed that number or distribution of data points was not sufficient to determine the value of m with any degree of precision and that very small population estimates accompanied by excessively large q values were being obtained.

The first problem was handled by setting $m = 2$, since the symmetric or Schaefer model seemed best in face of the uncertainty. The catchability coefficient was fixed at a value which minimized the sum of the squared deviations between GENPROD'S estimates of $P(t)$ and research vessel cruise estimates of population biomass at seven time points when both were available. The research vessel biomass estimates were obtained from surveys conducted in the spring and fall of 1965, 1966, and 1967 and the fall of 1968 (Gotshall, in press). Gotshall's catch in weight per standard haul was expanded on an areal basis to provide estimates for the entire survey area; as mentioned previously, these are negatively biased. Based on this procedure, $q = 8.5 \times 10^{-5}$ was the best value. The final fit of the Schaefer model was made with GENPROD's computing parameters KK and N set equal to 5 and 10, respectively. KK is related to the fineness of the surface searching procedure, and N involves the accuracy of the numerical integration used to estimate expected catch. These computing parameters are explained fully in Pella and Tomlinson (1969).

GENPROD estimated a maximum equilibrium catch (C_{max}) of 2.46 million pounds, an effort level required to obtain this catch under equilibrium conditions (F_{opt}) of 6,049 otter trawl

TABLE 1.—Estimates of Schaefer model parameters, observed catch and effort, predicted population size and catch, population and catch in millions of pounds, effort in thousands of hours.

Time interval		Population size end of interval	Applied effort	Observed catch	Predicted catch	Catch/effort	
Begin	End					Observed	Predicted
May 54	Aug. 54	8.63	0.206	0.169	0.150	0.819	0.727
Sept. 54	Apr. 55	9.07	0.0	0.0	0.0		
May 55	Oct. 55	8.82	0.733	0.505	0.557	0.689	0.760
Nov. 55	Apr. 56	9.11	0.0	0.0	0.0		
May 56	Sept. 56	8.57	1.11	0.896	0.836	0.803	0.750
Oct. 56	Apr. 57	9.00	0.0	0.0	0.0		
May 57	Oct. 57	8.59	1.05	0.748	0.783	0.713	0.746
Nov. 57	Apr. 58	8.96	0.0	0.0	0.0		
May 58	Sept. 58	8.18	1.61	1.14	1.17	0.706	0.726
Oct. 58	Apr. 59	8.76	0.0	0.0	0.0		
May 59	Sept. 59	7.83	2.01	1.69	1.41	0.841	0.702
Oct. 59	Mar. 60	8.45	0.0	0.0	0.0		
Apr. 60	Oct. 60	7.36	2.90	1.80	1.93	0.623	0.667
Nov. 60	May 61	8.22	0.0	0.0	0.0		
Jun. 61	Nov. 61	7.75	1.70	1.46	1.15	0.859	0.677
Dec. 61	Mar. 62	8.21	0.0	0.0	0.0		
Apr. 62	Oct. 62	6.39	4.70	2.98	2.87	0.635	0.611
Nov. 62	Mar. 63	7.23	0.0	0.0	0.0		
Apr. 63	Oct. 63	5.82	4.85	2.30	2.66	0.475	0.549
Nov. 63	Apr. 64	6.91	0.0	0.0	0.0		
May 64	Oct. 64	6.63	2.28	1.20	1.31	0.525	0.575
Nov. 64	Apr. 65	7.56	0.0	0.0	0.0		
May 65	Oct. 65	6.17	4.14	1.62	2.39	0.392	0.578
Nov. 65	Apr. 66	7.20	0.0	0.0	0.0		
May 66	Oct. 66	6.13	3.76	1.61	2.12	0.427	0.563
Nov. 66	Feb. 67	6.85	0.0	0.0	0.0		
Mar. 67	Oct. 67	6.22	3.71	2.26	2.05	0.608	0.553
Nov. 67	Apr. 68	7.24	0.0	0.0	0.0		
May 68	Oct. 68	6.72	2.54	2.67	1.50	1.052	0.592
Nov. 68	Feb. 69	7.36	0.0	0.0	0.0		
Mar. 69	Oct. 69	6.03	4.82	3.11	2.71	0.644	0.563
Nov. 69	Apr. 70	7.09	0.0	0.0	0.0		

Parameter estimates

C_{max}	F_{opt}	P_{opt}	q	U_{opt}	U_{max}	r	P_{max}	H	K
2.46	6.05	4.79	8.5×10^{-5}	0.407	0.814	0.884	9.58	-1.07×10^{-7}	−1.03

hours, and an optimum population size (P_{opt}) of 4.79 million pounds. Other parameter estimates, as defined by Pella and Tomlinson, and the complete output from the program are shown in Table 1.

Figure 1 shows both the expected catch as predicted by the model and the observed catch plotted against time. The fit appears to be generally quite good, although it has worsened during the most recent 5 years. The statistic R, derived by Pella and Tomlinson to measure the improvement in estimating catch from this model rather than from the mean catch, was 0.91. However, a somewhat spurious R is obtained when intervals with no catch are included in the data. This occurs because the model always predicts a zero catch from zero effort and the arithmetic mean cannot make such a prediction. Recalculating R from only periods when effort was applied yielded 0.75.

Figure 2 shows the fitted line ($m = 2$) for catch per unit effort versus effort in the equilibrium state and the observed catches per hour by year. However, the population should not

have been in equilibrium during the period studied since the level of effort fluctuated from year to year.

The actual catch exceeded the estimated maximum equilibrium yield (2.46 million pounds)

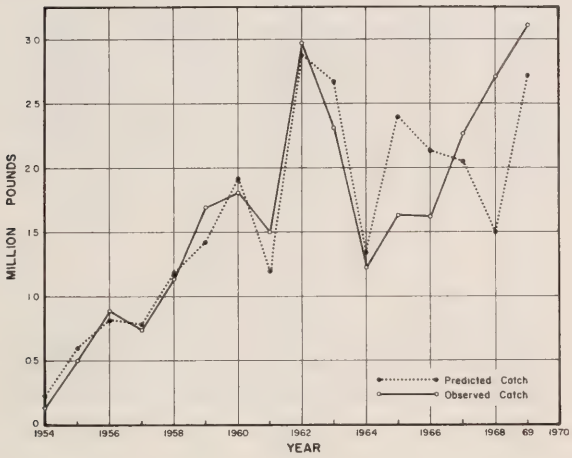

FIGURE 1.—Ocean shrimp catches predicted by GENPROD and observed catches for the years 1954 through 1969.

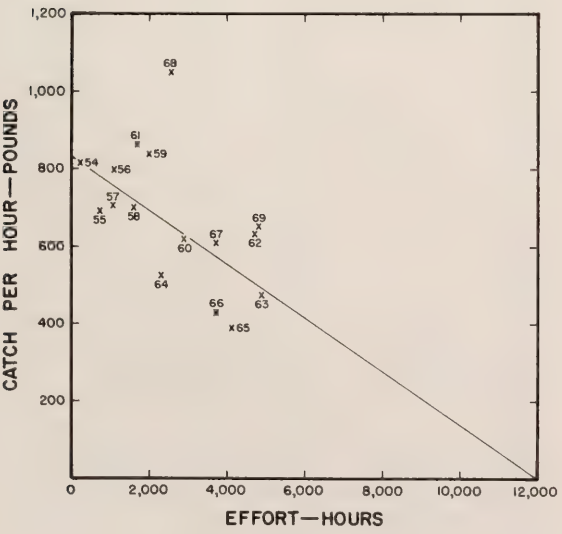

FIGURE 2.—Fitted model ($m = 2$) for catch-per-hour as a function of hours under equilibrium conditions.

during the period 1954 through 1969 only three times (Table 1): 1962, 1968, and 1969. Effort has always been substantially below the estimated level which would produce the maximum sustainable yield. A literal interpretation of these results would indicate the population has been underexploited until recently.

It is a problem in actual management situations to deduce how well a model such as this represents a population. In years when the observed catch-per-unit effort deviates substantially from the corresponding expected value, it cannot be determined whether deviations are due to an actual departure from the expected population size or due to a temporary change in the catchability. In the management strategy which we will discuss later, we are assuming the population size is being predicted correctly by the model and we are essentially ignoring deviations between the observed and expected catch insofar as they may represent actual population deviations.

DYNAMIC POOL MODEL

Catch data by age categories, both in weight and numbers, were utilized to estimate mortality, growth, and recruitment parameters necessary in a dynamic pool model.

AGE-STRUCTURED CATCH DATA

Catches from the population were landed at Eureka and Crescent City, Calif., and Brookings, Oreg. Landings data were obtained mainly from the Pacific Marine Fisheries Commission Data Series (1965-1969). Catches south of the California-Oregon border were recorded in that publication in tables for PMFC Area 96, but those from north of the border were included in, but did not comprise all of, the catch reported from PMFC Area 88. Catches within PMFC Area 88 south of the Rogue River were obtained from the Oregon Fish Commission (Jack Robinson, Oregon Fish Commission, personal communication). Catches made in the more recent years were obtained from the California Department of Fish and Game Shellfish Program (Daniel Gotshall and Walter Dahlstrom, California

Department of Fish and Game, personal communication). Virtually all catches were made during single day trips.

Landings were stratified into port-months, with Eureka-Crescent City as "California" and Brookings as "Oregon." Relative age frequency and weight at age were determined from samples of most port-month catches. Values used for California strata not sampled were either the average of preceding and following strata or the nearest sampled strata of the same season. The Oregon Fish Commission provided values for all Oregon strata.

Several methods of drawing samples from within strata were used by California. For all but very recent years, the methods were equivalent to assuming a simple random sample of shrimp from within strata. These sampled shrimp were aged by carapace length measurements, and the fraction falling into a specific age group determined its relative frequency. In recent years a simple random sample of boatloads was assumed drawn, and the length composition of a subsample from each boatload was weighted by the estimated number of shrimp in the load. Estimates by strata, done separately for Oregon and California, were combined to obtain the values in Table 2.

The average weight at age was determined by two methods: (1) the aged shrimp were placed into length frequency groups, a length-weight key was used to convert length to weight, and average weight for each age group was calculated; (2) the aged shrimp were weighed and an average weight computed directly for each age group. The study of aged catch data was performed for the 1955 through 1968 seasons. All aged shrimp fell into age groups 0, I, II, or III, but the 0 group was rare and omitted from the study.

Catch by age category for 2,598 million shrimp (22.88 million pounds) harvested during 1955 through 1968 are listed by month in Table 2. During the first 7 of these years, the fishery was active during 39 months and captured an estimated 954 million shrimp, excluding age 0, yielding a monthly average of 24.5 million. These shrimp weighed about 8.25 million pounds, averaging 212,000 lb. per month of fishing and 0.0086 lb. per shrimp. The fishery was active during 46 months of the second 7 years and caught an estimated 1,644 million shrimp, excluding age 0, for a monthly average of 35.7 million. These weighed about 14.63 million pounds, averaging 318,000 lb. per month and 0.0089 lb. per shrimp. The relative frequencies in numbers during the first 7 years were: 0.559 for age I, 0.422 for age II, and 0.019 for age III. During the second 7 years the frequencies were 0.495 for age I, 0.463 for age II, and 0.042 for age III. The reliability of the age frequency values is uncertain due to the aging method.

GROWTH CURVE

A growth in weight curve was obtained empirically by plotting average weights of shrimp by month and age for all seasons 1955 through 1968 (Tables 2 and 3, Figure 3). Dahlstrom (1970) and Gotshall (California Department of

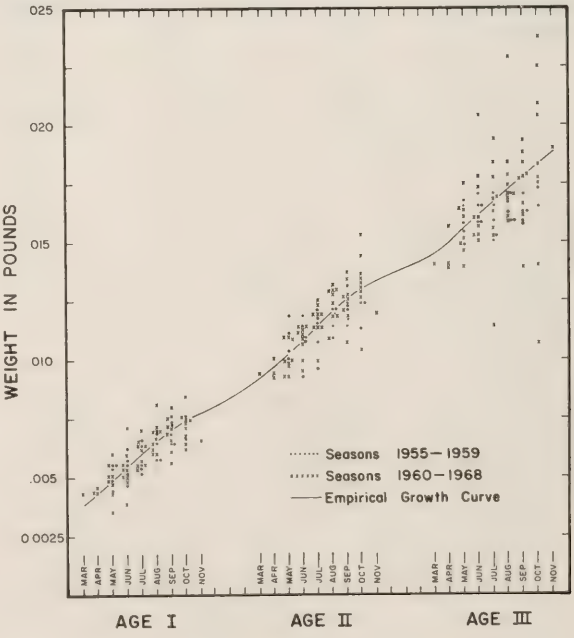

FIGURE 3.—Ocean shrimp growth in weight by month from sampling commercial landings. Seasons included are 1955 through 1968.

TABLE 2.—Aged catch[1] and catch-per effort (C.P.E.) statistics.
[Pounds and numbers in thousands.]

Season	Month	Age group	Relative frequency	Average weight (lb.)	C.P.E. numbers	Pounds	Numbers
1955	May	I	0.226	0.0055	9.9	4.3	782
		II	.747	.0118	32.7	30.4	2586
		III	.027	.0169	1.2	1.6	93
	June	I	.408	.0046	26.2	21.0	4531
		II	.576	.0118	37.0	75.3	6397
		III	.016	.0172	1.0	3.1	178
	July	I	.425	.0055	38.4	30.8	5603
		II	.565	.0122	51.0	90.8	7449
		III	.010	.0172	.9	2.3	132
	Aug.	I	.378	.0057	28.8	28.0	4897
		II	.603	.0122	46.0	95.3	7812
		III	.019	.0172	1.4	4.2	246
	Sept.	I	.588	.0064	49.9	47.7	7441
		II	.397	.0123	33.7	62.0	5024
		III	.015	.0172	1.3	3.3	190
	Oct.	I	.588	.0067	19.3	2.1	309
		II	.397	.0125	13.0	2.6	208
		III	.015	.0175	.5	.1	8
1956	May	I	.342	.0044	45.2	19.7	4479
		II	.608	.0099	80.4	78.8	7963
		III	.050	.0156	6.6	10.2	655
	June	I	.140	.0051	13.1	16.1	3166
		II	.833	.0093	78.2	174.4	18839
		III	.027	.0159	2.5	9.7	611
	July	I	.140	.0051	13.0	13.7	2697
		II	.843	.0097	78.5	157.7	16240
		III	.017	.0154	1.6	5.0	327
	Aug.	I	.161	.0057	13.0	27.8	4857
		II	.818	.0110	66.0	271.2	24680
		III	.021	.0169	1.7	10.7	634
	Sept.	I	.230	.0064	11.4	14.2	2221
		II	.753	.0115	37.3	83.6	7271
		III	.017	.0164	.8	2.7	164
1957	May	I	.366	.0053	29.5	22.0	4159
		II	.629	.0104	50.7	74.4	7147
		III	.005	.0167	.4	.9	57
	June	I	.592	.0057	33.4	21.9	3807
		II	.403	.0110	22.7	28.5	2592
		III	.005	.0167	.3	.5	82
	July	I	.592	.0063	33.0	11.2	1785
		II	.403	.0116	22.5	14.1	1215
		III	.005	.0167	.3	.3	15
	Aug.	I	.652	.0070	60.9	229.0	32515
		II	.343	.0122	32.0	208.6	17105
		III	.005	.0161	.5	4.0	249
	Sept.	I	.597	.0072	40.0	52.4	7235
		II	.386	.0122	25.8	57.0	4678
		III	.017	.0161	1.1	3.3	206
	Oct.	I	.597	.0074	50.9	9.0	1221
		II	.386	.0125	32.9	9.9	790
		III	.017	.0167	1.4	.6	35
1958	May	I	.429	.0048	30.1	41.6	8648
		II	.541	.0101	38.0	110.0	10906
		III	.030	.0150	2.1	9.1	609
	June	I	.429	.0055	37.2	82.3	14987
		II	.541	.0108	46.9	203.2	18899
		III	.030	.0159	2.6	16.6	1048
1958	July	I	.492	0.0053	29.7	30.9	5842
		II	.496	.0108	29.9	63.3	5890
		III	.012	.0152	.7	2.2	142
	Aug.	I	.596	.0064	64.8	121.7	18992
		II	.394	.0115	42.9	144.3	12555
		III	.010	.0161	1.1	5.1	319
	Sept.	I	.786	.0068	70.8	209.9	30649
		II	.209	.0118	18.8	95.9	8150
		III	.005	.0159	.5	3.1	195
1959	May	I	.599	.0055	87.2	104.0	18919
		II	.355	.0112	51.7	126.0	11213
		III	.046	.0159	6.7	23.1	1453
	June	I	.748	.0062	87.8	268.8	43542
		II	.240	.0115	28.2	160.6	13971
		III	.012	.0167	1.4	11.6	699
	July	I	.595	.0066	53.1	211.4	31921
		II	.382	.0118	34.1	241.1	20494
		III	.023	.0161	2.1	19.9	1234
	Aug.	I	.648	.0069	47.9	91.1	13120
		II	.329	.0120	24.3	80.3	6661
		III	.023	.0164	1.7	7.6	466
	Sept.	I	.720	.0073	66.8	207.3	28403
		II	.258	.0123	23.9	125.7	10178
		III	.022	.0164	2.0	14.2	868
1960	May	I	.601	.0042	45.1	48.2	11464
		II	.382	.0100	28.7	73.2	7287
		III	.017	.0153	1.3	5.0	324
	June	I	.689	.0050	53.2	94.0	18882
		II	.289	.0115	22.3	91.5	7920
		III	.022	.0162	1.7	9.8	603
	July	I	.798	0055	78.5	321.7	58428
		II	.192	.0114	18.9	160.5	14058
		III	.010	.0172	1.0	12.6	732
	Aug.	I	.700	.0060	63.4	281.4	47073
		II	.276	.0110	25.0	204.0	18560
		III	.024	.0162	2.2	26.1	1614
	Sept.	I	.699	.0066	53.5	210.6	31760
		II	.264	.0122	20.2	146.6	11995
		III	.037	.0168	2.8	28.3	1681
	Oct.	I	.698	.0076	33.3	51.3	6790
		II	.280	.0132	13.4	35.9	2724
		III	.022	.0179	1.0	3.8	214
1961	June	I	.454	.0052	48.8	52.3	10053
		II	.531	.0112	57.1	131.5	11759
		III	.015	.0162	1.6	5.4	332
	July	I	.441	.0063	36.1	79.0	12559
		II	.549	.0126	44.9	196.7	15635
		III	.010	.0170	.8	4.8	285
	Aug.	I	.337	.0069	25.8	118.9	17195
		II	.643	.0131	49.2	428.3	32809
		III	.020	.0172	1.5	17.6	1021
	Sept.	I	.400	.0076	31.6	62.0	8152
		II	.574	.0135	45.3	158.1	11698
		III	.026	.0190	2.1	10.1	530
	Oct.	I	.222	.0073	15.7	23.4	3181
		II	.758	.0146	53.5	158.5	10860
		III	.020	.0227	1.4	6.5	287

TABLE 2.—Continued.

Season	Month	Age group	Relative frequency	Average weight (lb.)	C.P.E. numbers	Pounds	Numbers
1961	Nov.	I	.633	0.0066	33.1	4.8	728
		II	.345	.0121	18.0	4.8	397
		III	.022	.0192	1.2	.5	25
1962	Apr.	I	.460	.0043	38.6	44.8	10512
		II	.465	.0093	39.1	99.0	10626
		III	.075	.0141	6.3	24.1	1714
	May	I	.460	.0047	41.8	121.8	25684
		II	.465	.0100	42.3	259.1	25964
		III	.075	.0148	6.8	62.0	4188
	June	I	.460	.0050	30.9	80.2	15998
		II	.465	.0113	31.2	182.9	16172
		III	.075	.0180	5.0	46.8	2608
	July	I	.414	.0053	22.4	86.4	16208
		II	.537	.0120	29.0	253.3	21024
		III	.049	.0179	2.6	34.3	1918
	Aug.	I	.560	.0059	32.6	249.2	42011
		II	.395	.0129	23.0	382.9	29633
		III	.045	.0231	2.6	78.0	3376
	Sept.	I	.560	.0068	41.2	281.6	41305
		II	.410	.0128	30.2	387.7	30241
		III	.030	.0180	2.2	39.7	2213
	Oct.	I	.550	.0064	51.3	95.1	14976
		II	.380	.0136	35.4	140.8	10347
		III	.070	.0177	6.5	33.7	1906
1963	Apr.	I	.160	.0043	11.2	7.5	1751
		II	.770	.0094	54.0	79.3	8427
		III	.070	.0142	4.9	10.9	766
	May	I	.162	.0034	10.6	20.7	6028
		II	.750	.0092	49.0	257.7	27909
		III	.088	.0177	5.7	57.9	3275
	June	I	.171	.0038	8.9	26.1	6811
		II	.730	.0096	37.9	280.4	29077
		III	.099	.0155	5.1	61.1	3943
1963	July	I	.165	.0055	6.8	39.5	7236
		II	.725	.0114	29.7	361.7	31796
		III	.110	.0154	4.5	74.4	4824
	Aug.	I	.274	.0061	11.1	99.6	16226
		II	.674	.0125	27.3	497.1	39915
		III	.052	.0176	2.1	54.1	3079
	Sept.	I	.289	.0061	12.5	46.8	7687
		II	.661	.0119	28.7	209.3	17582
		III	.050	.0163	2.2	21.7	1330
	Oct.	I	.330	.0068	14.4	20.1	2943
		II	.660	.0127	28.9	74.8	5886
		III	.010	.0108	.4	1.0	89
1964	May	I	.460	.0059	26.4	65.6	11102
		II	.523	.0110	30.1	139.3	12622
		III	.017	.0165	1.0	6.8	410
	June	I	.430	.0071	23.5	95.2	13352
		II	.550	.0107	30.0	182.3	17078
		III	.020	.0206	1.1	12.8	621
	July	I	.505	.0069	24.1	68.8	9924
		II	.474	.0124	22.6	115.9	9315
		III	.021	.0196	1.0	8.1	413
	Aug.	I	.548	.0081	30.4	183.7	22554
		II	.431	.0132	23.9	233.4	17739
		III	.021	.0186	1.2	16.0	864
1964	Sept.	I	.548	0.0071	29.5	9.7	1359
		II	.431	.0128	23.2	13.7	1069
		III	.021	.0179	1.1	.9	52
	Oct.	I	.548	.0076	26.7	17.8	2351
		II	.431	.0131	21.0	24.3	1849
		III	.021	.0186	1.0	1.7	90
1965	May	I	.612	.0049	29.4	98.2	20029
		II	.275	.0098	13.2	88.4	9000
		III	.113	.0141	5.4	52.3	3698
	June	I	.704	.0048	47.7	168.8	35439
		II	.266	.0109	18.0	146.3	13390
		III	.030	.0154	2.0	23.3	1510
	July	I	.868	.0056	61.5	456.1	81360
		II	.119	.0115	8.4	128.8	11154
		III	.013	.0164	.9	19.9	1219
	Aug.	I	.858	.0069	35.6	177.7	25734
		II	.126	.0130	5.2	49.1	3779
		III	.016	.0172	.7	8.2	480
	Sept.	I	.865	.0075	30.9	105.2	14112
		II	.124	.0132	4.4	26.7	2023
		III	.011	.0185	.4	3.3	179
	Oct.	I	.807	.0074	30.6	48.7	6545
		II	.176	.0137	6.7	19.5	1427
		III	.017	.0211	.6	2.9	138
1966	May	I	.147	.0050	7.2	11.4	2273
		II	.795	.0093	38.9	114.4	12295
		III	.058	.0151	2.8	13.5	897
	June	I	.230	.0053	11.1	70.7	13397
		II	.735	.0100	35.6	426.8	42812
		III	.035	.0158	1.7	32.2	2039
	July	I	.252	.0062	13.4	94.5	15364
		II	.717	.0100	38.1	437.6	43714
		III	.031	.0116	1.6	22.0	1890
	Aug.	I	.292	.0064	9.9	33.4	5223
		II	.687	.0119	23.3	146.1	12289
		III	.021	.0161	.7	6.1	376
	Sept.	I	.410	.0072	12.6	36.1	5022
		II	.586	.0127	18.0	91.4	7178
		III	.004	.0181	.1	.9	49
	Oct.	I	.424	.0072	15.8	19.4	2682
		II	.567	.0134	21.1	47.9	3587
		III	.009	.0206	.3	1.2	57
1967	Mar.	I	.674	.0042	51.7	10.4	2482
		II	.159	.0094	12.2	5.5	586
		III	.167	.0142	12.8	8.7	615
	Apr.	I	.730	.0044	60.7	45.6	10444
		II	.176	.0101	14.6	25.5	2518
		III	.094	.0158	7.8	21.2	1345
	May	I	.723	.0048	47.3	11.9	2461
		II	.176	.0110	11.5	6.6	599
		III	.101	.0162	6.6	5.6	344
	June	I	.739	.0055	61.8	294.7	53862
		II	.225	.0115	18.8	188.9	16399
		III	.036	.0152	3.0	39.8	2624
	July	I	.804	.0063	79.0	672.5	106859
		II	.172	.0120	16.9	273.8	22860
		III	.024	.0157	2.4	50.2	3190

TABLE 2.—Continued.

Season	Month	Age group	Relative frequency	Average weight (lb.)	C.P.E. numbers	Pounds	Numbers
1967	Aug.	I	.868	0.0071	61.9	359.7	50317
		II	.107	.0131	7.6	81.5	6203
		III	.025	.0171	1.8	24.7	1449
	Sept.	I	.840	.0079	30.0	76.8	9734
		II	.130	.0138	4.6	20.8	1506
		III	.030	.0195	1.1	6.8	348
	Oct.	I	.784	.0084	24.4	15.1	1807
		II	.171	.0154	5.3	6.1	394
		III	.045	.0239	1.4	2.5	104
1968	May	I	.193	.0054	17.1	77.9	14303
		II	.726	.0109	64.4	584.2	53801
		III	.081	.0166	7.2	99.4	6003
	June	I	.268	.0059	46.6	153.0	26091
		II	.715	.0112	124.3	776.9	69609
		III	.017	.0175	3.0	28.9	1655
1968	July	I	.380	0.0065	40.9	154.7	23947
		II	.611	.0120	65.7	460.6	38504
		III	.009	.0186	1.0	10.5	567
	Aug.	I	.277	.0066	15.0	46.1	6982
		II	.685	.0120	37.1	206.8	17267
		III	.038	.0180	2.1	17.2	958
	Sept.	I	.161	.0056	9.4	4.2	761
		II	.814	.0108	47.5	41.6	3848
		III	.025	.0141	1.5	1.7	118
	Oct.	I	.164	.0062	10.1	.5	81
		II	.812	.0105	50.2	4.2	402
		III	.024	.0142	1.5	.2	12

[1] Catches of 0 age groups are not included.

TABLE 3.—Average weight in pounds by age. From aged catch landed in northern California and southern Oregon, 1955-1968.

Month	Age I	Age II	Age III
March	0.0038	0.0092	0.0146
April	.0043	.0098	.0152
May	.0049	.0104	.0158
June	.0055	.0110	.0164
July	.0060	.0116	.0168
August	.0060	.0121	.0174
September	.0065	.0127	.0180
October	.0070	.0132	.0185
November	.0074	.0135	.0190
January	.0086	.0140	

Fish and Game, personal communication) indicated that shrimp grow faster in the open season than during the closed season. Hence, the empirical curve was drawn to show seasonal differences in the growth rate. A more objective fit of the data could be obtained, but it would not alter the results enough to change the conclusions contained herein.

The curve shows relatively constant (linear) growth in weight during the open season, but slower growth during the closed period. The shrimp apparently do not approach an asymptotic weight prior to reaching maximum age in the fishery, and growth in weight could be described as linear during the exploited phase. Obviously, there was considerable variation, increasing with age.

Annual average count per pound for ages I, II, and III combined varied from 94 in 1961 to 142 in 1965 (Figure 4). Monthly values varied from 76 to 155 with an average for all years of 114.

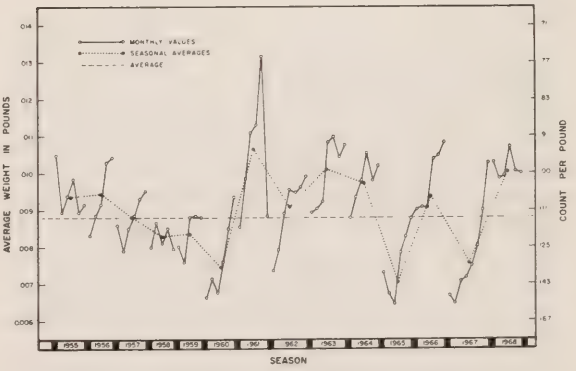

FIGURE 4.—Average size of ocean shrimp in the landings by month, season, and overall.

Because of the variation exhibited by the size at age data, it is possible that significant random or systematic errors are contained in the age composition data and that the subsequent analyses of these data will be correspondingly affected.

PARAMETER ESTIMATION WITH THE MURPHY METHOD

Reference Values

We used the generalized Murphy catch equation (Tomlinson, 1970) to analyze aged catch data. Gotshall (in press) provides estimates of natural mortality and biomass based upon a fishery independent randomized trawling scheme (Abramson, 1968). Since the biomass estimates are inherently negatively biased regardless of the catchability of shrimp and the mortality estimates may deviate from the population parameters in either direction, we decided to choose a natural mortality which would provide Murphy Method biomass estimates of a magnitude similar to those obtained from the randomized trawling scheme.

An annual natural mortality coefficient of $M = 1.44$ applied to all age groups yielded the appropriate biomass estimates. This is within the range of the M values given in Gotshall's (in press) Table 6 and cannot be considered significantly different from those estimates in view of the sizes of the standard errors shown in his Table 9.

Constructing Catch Ratios

Ratios of number caught in month $i+1$ to number caught in month i were calculated for all age III catches, giving values useful for within-season estimation of fishing mortality. To estimate across the closed seasons, the ratio of catch at age III in the first catch-month of season $i+1$ to catch at age II in the last catch-month of season i was calculated. For example, with 2 seasons and 3 months in each season, the ratios computed by this scheme would be: $R(1) = C_{III}(2)/C_{III}(1)$; $R(2) = C_{III}(3)/C_{III}(2)$; $R(3) = C_{III}(4)/C_{II}(3)$; $R(4) = C_{III}(5)/C_{III}(4)$; $R(5) = C_{III}(6)/C_{III}(5)$, where the catches used represent monthly catches by age (Table 4) and a closed season exists between months 3 and 4.

An additional assumption is that the exploitation rate (E) during the last month of each season is equal for ages II and III. Thus in the example, $E_{II}(3) = E_{III}(3)$. This assumption is necessary to allow estimation across the closed season.

Using these ratios for age III within season and age III to age II between seasons and assuming various exploitation rates for the last month of fishing in 1968, it was possible to make numerous estimates of the exploitation rates at age III during each month of fishing from 1955 to 1968. The Murphy method with backward calculation (Tomlinson, 1970) was used. The technique is similar to one used by Murphy (1965, 1966), except that Murphy used years instead of months, combined some age groups within years, had no years without catches, and did not treat year classes separately.

The data were separated into catches from year classes 1952 through 1967. Using the same hypothetical example as before (Table 4), the catch data can be put in the order $C_I(1)$, $C_I(2)$, $C_I(3)$, 0, $C_{II}(4)$, $C_{II}(5)$, $C_{II}(6)$, 0, $C_{III}(7)$, $C_{III}(8)$, $C_{III}(9)$. The catch ratios are computed as $C_I(2)/C_I(1)$, $C_I(3)/C_I(2)$, 0, $C_{II}(4)/C_I(3)$, $C_{II}(5)/C_{II}(4)$, $C_{II}(6)/C_{II}(5)$, 0, $C_{III}(7)/C_{II}(6)$, $C_{III}(8)/C_{III}(7)$, $C_{III}(9)/C_{III}(8)$. Since these catches all came from the same cohort, the Murphy method can be used to estimate $E_I(1)$, $E_I(2), \ldots, E_{III}(8)$, given that $E_{III}(9)$ is known. The previous analysis of age III data gave estimates of E at age III during the last month of fishing in each season, and these were used as starting values for backward calculation on each year class from 1952 through 1965. It was necessary in estimating E for the 1966 and 1967 year classes to choose values which gave an average population size in 1968 similar to the results obtained from fitting the Schaefer model.

Additional Modifications and Assumptions

Two additional assumptions fundamental to the results are: (1) ages II and III were exploited at the same rate, on the average, over the entire time period; (2) the catchability coefficient (q), computed as monthly catch-per-effort in weight divided by estimated average population weight for the combined age groups during the month, was reasonably constant over the entire time period. In order to satisfy these two assumptions, it was necessary to alter some

TABLE 4.—Hypothetical structure of age-structured shrimp catches and exploitation rates as arranged for analysis by the Murphy method.

Season	Catch-month	Catches by ages			Exploitation rates by ages		
		Age I	Age II	Age III	Age I	Age II	Age III
1	1	$C_I(1)$	$C_{II}(1)$	$C_{III}(1)$	$E_I(1)$	$E_{II}(1)$	$E_{III}(1)$
1	2	$C_I(2)$	$C_{II}(2)$	$C_{III}(2)$	$E_I(2)$	$E_{II}(2)$	$E_{III}(2)$
1	3	$C_I(3)$	$C_{II}(3)$	$C_{III}(3)$	$E_I(3)$	$E_{II}(3)$	$E_{III}(3)$
	Closed season						
2	4	$C_I(4)$	$C_{II}(4)$	$C_{III}(4)$	$E_I(4)$	$E_{II}(4)$	$E_{III}(4)$
2	5	$C_I(5)$	$C_{II}(5)$	$C_{III}(5)$	$E_I(5)$	$E_{II}(5)$	$E_{III}(5)$
2	6	$C_I(6)$	$C_{II}(6)$	$C_{III}(6)$	$E_I(6)$	$E_{II}(6)$	$E_{III}(6)$
	Closed season						
3	7	$C_I(7)$	$C_{II}(7)$	$C_{III}(7)$	$E_I(7)$	$E_{II}(7)$	$E_{III}(7)$
3	8	$C_I(8)$	$C_{II}(8)$	$C_{III}(8)$	$E_I(8)$	$E_{II}(8)$	$E_{III}(8)$
3	9	$C_I(9)$	$C_{II}(9)$	$C_{III}(9)$	$E_I(9)$	$E_{II}(9)$	$E_{III}(9)$

of the E values from the age III analysis used as starting values for the year class solutions.

An additional problem occurred which resulted in some final changes that were arbitrary and difficult to explain. For some years, especially 1955 through 1959, estimates of population size were quite low and q very high. It was demonstrated that a good transfer from age III to age II across the closed season did not occur for the year classes involved. Therefore, with year classes 1953 through 1958, 1962, 1963, and 1966, the estimation from the last catch-month at age II to the first catch-month at age I disregarded estimates during age III. It is hoped that the final result justifies these arbitrary decisions. It was also noted from the dots on Figure 3 that a growth curve from the sample data (Table 2) for seasons 1955 through 1959 indicates faster growth during the closed season than during the open season. This seems extremely doubtful in light of other contrary evidence and indicates that the problem was caused by inaccurate aging. Since age III shrimp make up such a small fraction of the catch and population biomass, it was not considered to seriously discredit final results.

Fishing Mortality Estimates

Estimation of monthly instantaneous fishing mortality coefficients, (F), was accomplished for each age group in each month by applying the Murphy method, as described above, to catches in numbers (Table 2). Since $M = 0.12$ was used as monthly instantaneous natural mortality for all months and ages, monthly exploitation rates, E, and monthly survival rates, s, may be obtained from

$$E = F\left[1 - e^{-(F+0.12)}\right]/(F + 0.12),$$

and

$$s = e^{-(F+0.12)}.$$

The estimates of F (Table 5) varied considerably, but age I was always exploited at a rate lower than ages II and III. During the 7 years, 1955-1961, average estimated F was 0.015 for age I, 0.056 for age II, and 0.057 for age III. In the 7 years, 1962-1968, $F(\text{I}) = 0.023$, $F(\text{II}) = 0.116$, and $F(\text{III}) = 0.159$. Averages for all 14 years were $F(\text{I}) = 0.019$, $F(\text{II}) = 0.088$, and $F(\text{III}) = 0.089$. Thus, as previously stated for a condition of estimation, ages II and III were exploited at about the same rates.

Converting fishing mortality to exploitation (Table 6), it was estimated that the fishery was removing about 5% of ages II and III and 1% of age I each month of fishing. Fishing intensity increased over the years and during 1962-1968 exploitation was nearly double that of 1955-1961 for each age. During the period 1961-1967, July and August were the most important months, followed by May, June, and September, while April and October were of little importance. Average F (Table 10) during these years, for

TABLE 5.—Monthly instantaneous fishing mortality coefficients.

Year	Month	Age group I	Age group II	Age group III
1955	May	0.001	0.011	0.006
	June	.003	.032	.013
	July	.004	.044	.011
	Aug.	.004	.055	.023
	Sept.	.007	.042	.021
	Oct.	.001	.002	.001
	Mean	.0033	.0310	.0125
1956	May	.003	.021	.042
	June	.002	.058	.046
	July	.002	.060	.029
	Aug.	.005	.112	.066
	Sept.	.003	.040	.020
	Mean	.0030	.0582	.0406
1957	May	.003	.022	.014
	June	.003	.009	.009
	July	.002	.005	.005
	Aug.	.038	.080	.096
	Sept.	.010	.026	.098
	Oct.	.002	.005	.020
	Mean	.0097	.0245	.0433
1958	May	.006	.039	.071
	June	.012	.081	.154
	July	.005	.030	.026
	Aug.	.020	.077	.068
	Sept.	.038	.060	.050
	Mean	.0162	.0574	.0738
1959	May	.016	.037	.090
	June	.042	.055	.053
	July	.036	.098	.113
	Aug.	.017	.038	.052
	Sept.	.043	.070	.120
	Mean	.0308	.0596	.0856
1960	May	.008	.030	.019
	June	.015	.038	.042
	July	.055	.080	.060
	Aug.	.052	.133	.168
	Sept.	.042	.109	.241
	Oct.	.010	.030	.040
	Mean	.0303	.0700	.0783
1961	June	.009	.048	.021
	July	.013	.077	.031
	Aug.	.020	.209	.137
	Sept.	.011	.098	.090
	Oct.	.005	.114	.059
	Nov.	.001	.005	.006
	Mean	.0098	.0918	.0590
1962	Apr.	.006	.034	.040
	May	.018	.099	.120
	June	.013	.016	.094
	July	.015	.122	.085
	Aug.	.045	.231	.193
	Sept.	.053	.354	.171
	Oct.	.022	.179	.200
	Mean	.0246	.1564	.1290
1963	Apr.	0.002	0.026	0.030
	May	.007	.105	.161
	June	.009	.140	.270
	July	.011	.204	.555
	Aug.	.029	.386	.762
	Sept.	.016	.267	.812
	Oct.	.007	.123	.100
	Mean	.0116	.1787	.3843
1964	May	.017	.071	.021
	June	.024	.119	.038
	July	.021	.080	.029
	Aug.	.055	.198	.072
	Sept.	.004	.015	.005
	Oct.	.008	.030	.010
	Mean	.0215	.0855	.0292
1965	May	.017	.069	.298
	June	.035	.128	.174
	July	.098	.137	.190
	Aug.	.037	.058	.098
	Sept.	.024	.036	.044
	Oct.	.013	.030	.040
	Mean	.0373	.0763	.1407
1966	May	.002	.057	.097
	June	.017	.262	.301
	July	.023	.423	.456
	Aug.	.009	.183	.140
	Sept.	.010	.142	.022
	Oct.	.006	.090	.030
	Mean	.0112	.1928	.1743
1967	Mar.	.001	.002	.030
	Apr.	.007	.011	.078
	May	.002	.003	.024
	June	.045	.100	.228
	July	.108	.180	.432
	Aug.	.063	.062	.325
	Sept.	.014	.018	.110
	Oct.	.003	.005	.040
	Mean	.0304	.0476	.1584
1968	May	.025	.098	.207
	June	.054	.162	.074
	July	.059	.116	.030
	Aug.	.020	.064	.060
	Sept.	.002	.017	.009
	Oct.	.001	.002	.001
	Mean	.0268	.0765	.0635

TABLE 6.—Monthly exploitation rates.

Year	Month	Age group I	Age group II	Age group III
1955	May	0.0004	0.0107	0.0056
	June	.0029	.0301	.0121
	July	.0041	.0408	.0103
	Aug.	.0040	.0505	.0218
	Sept.	.0069	.0387	.0194
	Oct.	.0003	.0019	.0009
1956	May	.0030	.0195	.0385
	June	.0024	.0531	.0422
	July	.0023	.0547	.0266
	Aug.	.0046	.0995	.0599
	Sept.	.0024	.0370	.0187
1957	May	.0031	.0203	.0134
	June	.0032	.0085	.0086
	July	.0017	.0045	.0046
	Aug.	.0349	.0720	.0860
	Sept.	.0091	.0241	.0883
	Oct.	.0017	.0047	.0187
1958	May	.0058	.0362	.0642
	June	.0114	.0736	.1346
	July	.0051	.0281	.0240
	Aug.	.0188	.0695	.0623
	Sept.	.0348	.0549	.0460
1959	May	.0146	.0346	.0812
	June	.0385	.0504	.0482
	July	.0332	.0881	.1011
	Aug.	.0160	.0356	.0482
	Sept.	.0396	.0638	.1067
1960	May	.0076	.0277	.0181
	June	.0141	.0350	.0387
	July	.0501	.0727	.0552
	Aug.	.0481	.1172	.1457
	Sept.	.0385	.0976	.2024
	Oct.	.0097	.0279	.0370
1961	June	.0083	.0442	.0290
	July	.0119	.0696	.0290
	Aug.	.0185	.1778	.1207
	Sept.	.0101	.0880	.0810
	Oct.	.0045	.1016	.0541
	Nov.	.0012	.0047	.0056
1962	Apr.	.0061	.0311	.0371
	May	.0171	.0885	.1064
	June	.0121	.0686	.0842
	July	.0140	.1084	.0767
	Aug.	.0416	.1946	.1657
	Sept.	.0483	.2820	.1485
	Oct.	.0208	.1550	.1712
1963	Apr.	0.0017	0.0246	0.0282
	May	.0067	.0943	.1402
	June	.0086	.1230	.2235
	July	.0104	.1744	.4037
	Aug.	.0267	.3028	.5062
	Sept.	.0147	.2211	.5282
	Oct.	.0064	.1090	.0898
1964	May	.0162	.0644	.0199
	June	.0223	.1054	.0347
	July	.0192	.0730	.0270
	Aug.	.0501	.1698	.0656
	Sept.	.0036	.0141	.0048
	Oct.	.0070	.0279	.0094
1965	May	.0162	.0629	.2433
	June	.0328	.1130	.1509
	July	.0880	.1206	.1635
	Aug.	.0346	.0528	.0878
	Sept.	.0222	.0338	.0407
	Oct.	.0119	.0279	.0370
1966	May	.0024	.0524	.0870
	June	.0160	.2179	.2458
	July	.0210	.3262	.3471
	Aug.	.0082	.1577	.1230
	Sept.	.0090	.1247	.0208
	Oct.	.0055	.0810	.0279
1967	Mar.	.0013	.0022	.0277
	Apr.	.0063	.0107	.0703
	May	.0017	.0029	.0219
	June	.0414	.0895	.1929
	July	.0968	.1554	.3323
	Aug.	.0573	.0569	.2622
	Sept.	.0133	.0166	.0983
	Oct.	.0028	.0050	.0370
1968	May	.0233	.0876	.1767
	June	.0492	.1409	.0676
	July	.0538	.1033	.0281
	Aug.	.0187	.0587	.0552
	Sept.	.0023	.0157	.0081
	Oct.	.0003	.0019	.0009

June to September, was 0.16 for age II, 0.21 for age III, and only 0.03 for age I.

Biomass Estimation

The Murphy method produces estimates of population size in numbers at the beginning of each catch interval. The present study also required estimates of biomass. Murphy (1966) stated he computed biomass by dividing the catch in weight by the appropriate estimate of E from his analysis of numbers in the catch. This would result in a positively biased biomass estimate, since it is equivalent to multiplying the number alive at the beginning of a catch interval by the average weight during the interval.

Two ways of computing the correct estimates of biomass utilizing Murphy's method to estimate numbers are possible:

(1) multiply the estimated average weight at the beginning of each interval by the number estimated for the population by the Murphy method. That is,

$\widehat{P^*_{ij}} = \hat{C}_{ij}\hat{\bar{w}}^*_{ij}/\hat{E}_{ij}$ = estimated biomass to begin interval j, age i,

$\hat{\bar{w}}^*_{ij}$ = estimated average weight for age i at beginning of interval j,

$\hat{C}_{ij}$ = estimated number of age i caught during interval j.

(2) Multiply the average number of age i alive during interval j by the average weight of age i individuals during this interval. That is,

$\hat{\bar{P}}_{ij} = \hat{\bar{N}}_{ij}\hat{\bar{w}}_{ij}$ = estimated average biomass of age i, during j.

$\hat{\bar{w}}_{ij}$ = average weight in the catch of age i, during interval j.

$\hat{\bar{N}}_{ij}$ = average number alive during interval j of age i.

For this study, the second method was used with average population numbers, $\hat{\bar{N}}_{ij}$, being given by

$$\hat{\bar{N}}_{ij} = \hat{N}_{ij}(1-e^{-t_j\hat{Z}_{ij}})/(t_j\hat{Z}_{ij})$$

$$\hat{N}_{ij} = \hat{C}_{ij}/\hat{E}_{ij},$$

t_j = fraction of year elapsed during interval j; $t_j = 1/12$ for all intervals.

$\hat{Z}_{ij}$ = total annual instantaneous mortality coefficient during j.

Total population biomass for ages I through III was computed as

$$\hat{\bar{P}}_j = \sum_{i=1}^{3} \hat{\bar{N}}_{ij}\hat{\bar{w}}_{ij} = \text{average biomass available during interval } j, \text{ and the}$$

catchability coefficient from

$$\hat{q}_j = \sum_{i=1}^{3} \hat{C}_{ij}\hat{\bar{w}}_{ij}/(\hat{\bar{P}}_j f_j); \; f_j \text{ is effort expended during interval } j.$$

Estimates of within-season monthly population biomass varied from a high of 12.0 million pounds in May 1955 to a low of 3.4 million pounds in October 1964 (Table 7). Population changes estimated by the Murphy method follow trends estimated by the Schaefer model (Figure 5), except Schaefer model estimates exhibit considerably less within season change. This difference in range of within season change was caused by the different ways in which the two models treat growth and recruitment. The Schaefer model assumes a continuous process for combined growth and recruitment, whereas the Murphy method treats growth as continuous (Figure 3) and recruitment as instantaneous (Table 7).

Estimates of monthly catchability (q) (Table 7) had extreme variation and showed an average within season increase (Figure 6). However, the within season changes were inconsistent and obscured by the variation. Monthly estimates of q varied from 21.3×10^{-5} in June 1968 to 3.8×10^{-5} in May 1955. Yearly averages had less variation and appeared to show no long-term trend (Figure 7). Average q over all months was about 9.0×10^{-5} which agreed closely with the value 8.5×10^{-5} used for the Schaefer model.

Spawning Biomass and Recruitment

Female spawning biomass consisted of all ages II and III shrimp plus some fraction of age I shrimp. Some data from commercial catch samples on the fraction of age I shrimp func-

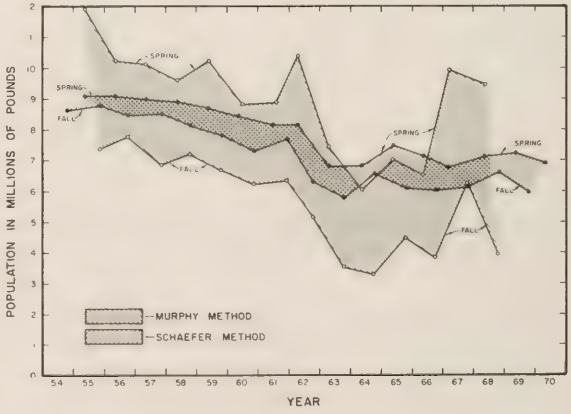

FIGURE 5.—Comparison of annual maximum and minimum population sizes as estimated by the Schaefer model and the Murphy method.

TABLE 7.—Ocean shrimp population biomass in thousands of pounds by age and month.

Year	Month	Ages I	Ages II	Ages III	Total	Est. $q \times 10^6$
1955	May	9,100	2,670	265	12,035	38
	June	6,788	2,318	237	9,343	61
	July	7,119	2,051	208	9,378	91
	Aug.	6,538	1,731	181	8,450	89
	Sept.	6,467	1,481	157	8,105	51
	Oct.	5,942	1,300	140	7,382	41
1956	May	6,265	3,770	246	10,281	107
	June	6,385	3,008	212	9,605	86
	July	5,649	2,637	175	8,461	101
	Aug.	5,619	2,432	164	8,215	101
	Sept.	5,570	2,089	134	7,793	66
1957	May	6,701	3,425	67	10,193	68
	June	6,434	3,155	58	9,647	46
	July	6,229	2,940	51	9,220	51
	Aug.	6,067	2,625	42	8,734	95
	Sept.	5,405	2,207	34	7,646	82
	Oct.	4,872	1,975	29	6,876	118
1958	May	6,710	2,811	129	9,650	58
	June	6,739	2,501	108	9,348	80
	July	5,704	2,096	84	7,884	62
	Aug.	6,053	1,885	75	8,013	116
	Sept.	5,574	1,598	62	7,234	99
1959	May	6,650	3,372	256	10,278	113
	June	6,441	2,922	222	9,585	93
	July	5,895	2,459	176	8,530	92
	Aug.	5,337	2,084	146	7,567	86
	Sept.	4,830	2,795	119	6,744	121
1960	May	5,987	2,453	255	8,695	57
	June	6,217	2,419	276	8,912	62
	July	5,894	2,001	209	8,104	82
	Aug.	5,378	2,537	155	7,070	97
	Sept.	5,048	1,343	117	6,508	100
	Oct.	4,967	1,196	96	6,259	71
1961	June	5,875	2,737	172	8,784	105
	July	6,234	2,566	155	8,955	90
	Aug.	5,983	2,054	128	8,165	104
	Sept.	5,749	1,614	112	7,475	119
	Oct.	4,885	1,391	110	6,386	145
	Nov.	3,893	960	80	4,933	93
1962	Apr.	6,888	2,956	601	10,445	59
	May	6,714	2,631	518	9,863	73
	June	6,197	2,424	500	9,121	66
	July	5,764	2,076	404	8,244	63
	Aug.	5,519	1,660	404	7,583	73
	Sept.	5,358	1,095	232	6,685	106
	Oct.	4,265	785	168	5,218	177
1963	Apr.	4,101	3,000	358	7,459	84
	May	2,892	2,448	360	5,700	104
	June	2,830	2,008	227	5,065	95
	July	3,546	1,772	134	5,452	81
	Aug.	3,466	1,289	71	4,826	92
	Sept.	2,979	785	27	3,791	120
	Oct.	2,939	609	10	3,558	132
1964	May	3,790	1,970	317	6,077	83
	June	3,972	1,538	341	5,851	87
	July	3,349	1,438	278	5,065	92
	Aug.	3,363	1,177	222	4,762	123
	Sept.	2,542	908	183	3,633	145
	Oct.	2,378	810	167	3,355	148
1965	May	5,676	1,281	176	7,133	49
	June	4,764	1,147	134	6,045	75
	July	4,657	942	105	5,704	80
	Aug.	4,751	852	84	5,687	57
	Sept.	4,409	732	75	5,216	57
	Oct.	3,831	651	73	4,555	73
1966	May	4,481	1,999	140	6,620	67
	June	4,131	1,628	107	5,866	75
	July	4,191	1,035	48	5,274	92
	Aug.	3,804	799	43	4,646	76
	Sept.	3,754	645	40	4,439	73
	Oct.	3,332	533	39	3,904	103
1967	Mar.	7,401	2,371	293	10,065	51
	Apr.	6,853	2,246	274	9,373	57
	May	6,708	2,154	236	9,098	51
	June	6,566	1,895	174	8,635	70
	July	6,212	1,522	116	7,850	94
	Aug.	5,741	1,309	76	7,126	80
	Sept.	5,407	1,172	62	6,641	48
	Oct.	5,049	1,148	62	6,259	51
1968	May	3,105	5,991	480	9,476	95
	June	2,853	4,804	389	8,046	213
	July	2,636	3,971	347	6,954	154
	Aug.	2,295	3,219	286	5,800	100
	Sept.	1,694	2,474	192	4,360	134
	Oct.	1,667	2,116	170	3,953	155

tioning as females were made available from unpublished sources, but a good method for predicting the fraction of age I shrimp that would function as females was not found. Thus, a simple mean was computed from the data available for years 1957 through 1967 (Table 8). It is assumed that this mean proportion (0.33) predicts the fraction of the biomass of age I shrimp alive in September that will be females and that the sum of the September biomass of ages II and III, plus the fraction of age I functioning as females in September, is directly proportional to spawning biomass during the spawning season.

Recruitment was defined as the number of age I shrimp alive on May 1 of each year. Thus, the female biomass in September of season i is proportional to the biomass which will spawn sometime prior to May of season $i+1$ and the progeny of this spawning will be recruited to the fishery at the beginning of season $i+2$. Two

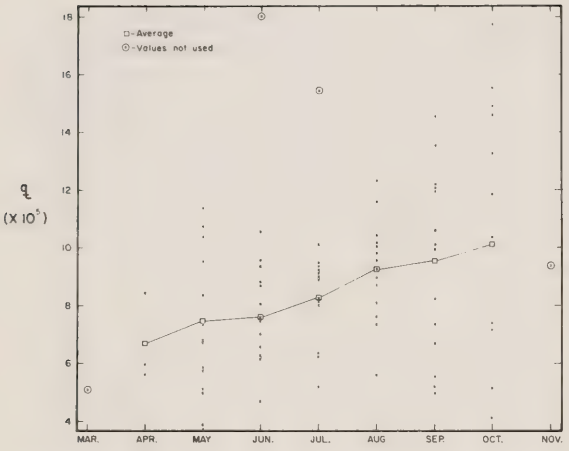

FIGURE 6.—Within-season changes in catchability coefficient (q). Line connects seasonal mean values. Circled points were not used to compute means.

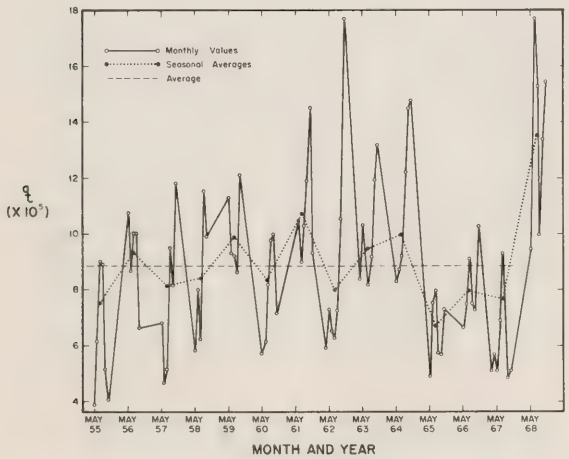

FIGURE 7.—Monthly catchability coefficients (q). Dashed line shows 1955-1968 mean.

TABLE 8.—Estimated percentage of numbers of shrimp functioning as spawners at age I.

Year	Percent	Year	Percent
1957	43	1963	21
1958	17	1964	36
1959	36	1965	51
1960	42	1966	24
1961	11	1967	54
1962	30	Mean	33

models for predicting recruitment from population biomass were tried.

$$\text{Model I}: \quad R_{i+2} = aS_i\, e^{-bS_i};$$

$$\text{Model II}: \quad R_{i+2} = cS_i\, e^{-dP_{i+1}}$$

where

R_{i+2} = number of age I shrimp on May 1, season $i+2$.

S_i = average biomass of functioning females during September of season i.

P_{i+1} = average total biomass (ages I, II, and III) during September of season $i+1$.

a, b, c, and d are constants.

Model I assumes the number of eggs produced is proportional to spawning biomass and that survival from egg to recruitment is influenced by this same spawning biomass. Model II assumes the number of eggs is proportional to spawning biomass and that survival from egg to recruit is a function of average biomass competing for the population space. September of season $i+1$ was selected for Model II because this seemed likely to be proportional to the average biomass encountered by age 0 shrimp, and data were available for all Septembers. May 1 was selected for recruitment since most seasons opened on this date.

Both models of recruitment were fitted by using transformations and a linear model (Paulik and Gales, 1965). The transformed equations are:

$$\text{Model I}: \log_e(R_{i+2}/S_i) = \log_e(a) - bS_i;$$

$$\text{Model II}: \log_e(R_{i+2}/S_i) = \log_e(c) - dP_{i+1}.$$

Estimates of recruitment by the Murphy method varied from a high of 1.5 billion shrimp on May 1, 1962, to a low of 0.6 billion on May 1, 1968. Spawning stocks producing recruitment varied from 4.5 million pounds in September 1959 to 1.8 million pounds in September 1963 (Table 9).

The range in recruitment observed at any given spawning stock size was very large relative to the range in size of spawning stock, and the fitting of Model I did not result in a meaningful

TABLE 9.—Recruits vs. spawners and population biomass.

Year (i)	[1] R_{i+2}	[2] S_i	[3] P_{i+1}
1955	1,341.6	3,772	7,793
1956	1,491.0	4,061	7,646
1957	1,295.8	4,025	7,234
1958	1,508.4	3,499	6,744
1959	[4] 1,365.6	4,508	6,508
1960	1,502.0	3,126	7,475
1961	899.7	3,623	6,685
1962	685.3	3,095	3,791
1963	1,236.4	1,795	3,633
1964	947.1	1,930	5,216
1965	1,447.6	2,262	4,439
1966	613.9	1,924	6,641

[1] R_{i+2} = Recruits in millions on May 1 of year $i+2$.
[2] S_i = Spawners in thousands of pounds during September of year i.
[3] P_{i+1} = Population in thousands of pounds during September of year $i+1$.
[4] Estimated from June.

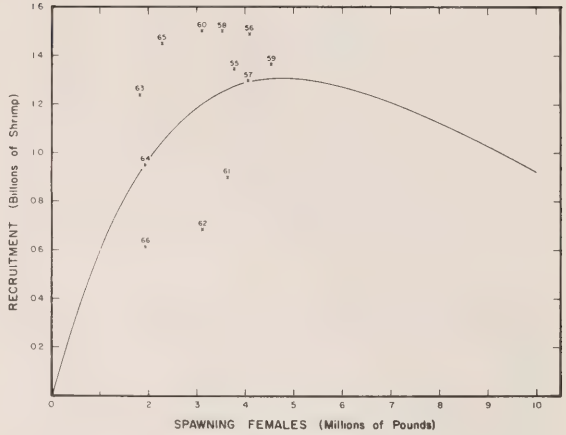

FIGURE 8.—Number of recruits on May 1 of year $i+2$ produced by spawning biomass of September, year i. Smooth curve represents Model I of the text.

relationship (Figure 8). Model II, which considers the effect of the population competing with the prerecruits, did not account for the variation in recruitment either. Consequently, a realistic spawner-recruit relationship could not be determined from the available data.

Yield per Recruit

Because a well-defined spawner-recruit relationship could not be determined the use of a self-generating model of the dynamic pool type, such as Walters (1969), is not feasible. We can, however, utilize the age-structured catch data to examine this type of model under the assumption that recruitment is constant.

We feel that the greatest confidence can be placed in the estimates of instantaneous fishing mortality (F_{ij}) for 1961 through 1967 (Table 5). For this reason, these values were combined to yield average monthly values ($\bar{F}_{ij}$). The averages were computed as simple arithmetic means to give vectors of average fishing mortality by month and age for April through October (Table 10), and allow for computations of yield per recruit. Yield per million recruits was computed by step-wise integration (Ricker, 1958; Paulik and Bayliff, 1967). For a season of l months, a year class would be exposed to fishing for $n = 3l$ months and protected for $3(12—l)$ months. This would give a total lifetime after recruitment of $L=36$ months. The yield can be expressed as

$$Y = \sum_{k=1}^{L} y_k = \sum_{i=1}^{3} \sum_{j=1}^{12} C_{ij}\bar{w}_{ij};\ k = 12(i—1) + j$$

where

$\bar{w}_{ij}$ = average weight taken from the empirical growth curve,
$C_{ij} = L_k E_{ij}$ = number caught in month j of year i,
$E_{ij} = \bar{F}_{ij}(1—e^{-Z_k})/Z_k$ = monthly exploitation rate in month j of year i
$Z_k = (\bar{F}_{ij} + M)$ = total monthly instantaneous mortality
(note that Z was previously used

TABLE 10.—Mean monthly instantaneous fishing mortality coefficients, $\bar{F}_{ij}$, by age group.

Month	Age group		
	I	II	III
April	0.005	0.024	0.049
May	.011	.067	.120
June	.022	.123	.162
July	.041	.175	.254
August	.037	.190	.247
September	.019	.133	.179
October	.009	.082	.068

to represent the annual mortality coefficient),

$L_k = R \exp\left[-\sum_{h=1}^{k-1} Z_h\right]$ = number survivors to begin interval k,

$Z_h = M$ during months closed to fishing.

R = number of recruits = 1,000,000.

M = 0.12.

The yields at various levels of fishing intensity were predicted by multiplying all $\bar{F}_{ij}$ by a constant equal to the intensity change desired and recalculating catches for all months. Estimates of expected yield in numbers and expected average weight per shrimp were also provided by this procedure. By setting appropriate values of $F = 0$, yields for various seasons and entry ages were computed.

If $M = 0.12$ is the monthly instantaneous mortality coefficient and if growth in weight at age is taken from the empirical growth curve (Table 3), a year class of shrimp that is not fished will reach its maximum biomass during the period July to August as age I. The biomass will then decline rapidly and by July to August as age II it will be about one-half the maximum.

The estimated yield per recruit for the period 1961 to 1967 was 0.00165 lb. per shrimp. Since the average annual catch during that 7-year period was 1.918 million pounds, it would have required an average of 1.162 billion recruits on April 1 to support the catch. The Murphy method estimates an average recruitment on May 1 of about 1.155 billion. Thus, the analysis of yield per recruit is in good agreement with the Murphy method results.

Given 1.155 billion recruits on April 1, it would require a yield per recruit of 0.00216 lb. per shrimp to obtain a total harvest approximately equal to the maximum sustainable yield estimated from the Schaefer model. To have obtained a yield-per-recruit of 0.00216 during those 7 years would have required an increase in fishing mortality of about 75% (Figure 9). This additional yield could not have been obtained by shortening the season or changing age at recruitment unless a substantial increase in fishing mortality accompanied the changes (Figures 9 and 10). With the distribution of fishing effort observed during 1961-1967, the average total monthly instantaneous fishing mortality ($\sum\sum F_{ij}$) operating against a year class during 3 seasons was estimated to be 2.0176. While maintaining total fishing mortality at 2.0176,

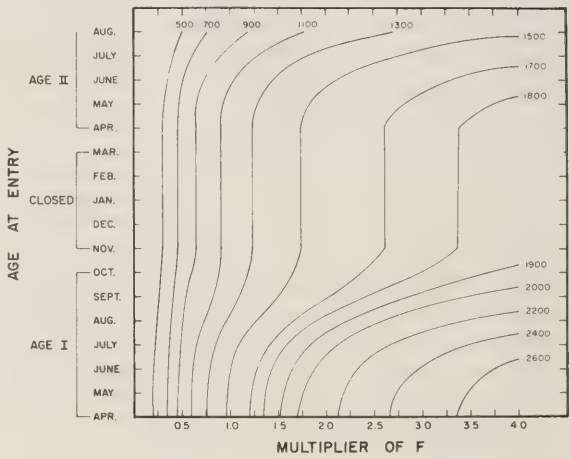

FIGURE 9.—Yield in pounds per million recruits as a function of age at entry into the fishery and fishing mortality. Fixed population parameters used were 1961-1967 means.

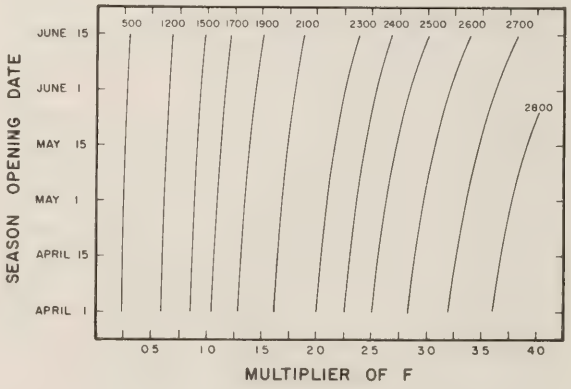

FIGURE 10.—Yield in pounds per million recruits as a function of season opening date and monthly fishing mortality coefficient. October 31 season closing date assumed and fixed population parameters used were 1961-1967 means.

the annual yield could theoretically be increased to about 2.8 million pounds by shifting fishing mortality so that I's and II's suffered equal rates. This would involve a 75% reduction in fishing mortality at ages II and III and assumes that the population with the new age structure would continue to produce 1,155 billion recruits. Such a change would also produce a reduction of 26% in the average size of shrimp in the catch and pose the problem of how the mortality pattern could be so altered.

INTER-MODEL COMPARISONS

Because we were unable to determine a spawner-recruit relationship and produce a self-generating form of the dynamic pool model, a realistic comparison of the results from the two types of models is not possible. In addition, the yield-per-recruit model treats natural mortality and growth parameters as constant while in the Schaefer model they are components of density dependent terms.

It is of interest to note that the biomass estimates obtained from the age-structured catch data by the Murphy method are in general agreement with the corresponding estimates of the Schaefer model. Although this does not compare the yield-per-recruit and Schaefer models, we feel it indicates some support of the Schaefer model from a semi-independent source. Another point of agreement between the yield-per-recruit and Schaefer models was that, given the average recruitment over the 1961-67 period, the former required a 75% increase in fishing mortality to produce the Schaefer model's maximum sustainable yield while the average annual effort expended during that period would require a 68% increase to reach the optimum effort level of the Schaefer model. However, as can be seen from Figure 9, maximum yield-per-recruit is predicted to occur at a much higher effort level under the previously mentioned assumption of constant parameters.

It seems clear from the foregoing discussion of results relative to the two models that management procedures should be based on the Schaefer model at the present time.

PROPOSED MANAGEMENT STRATEGY

Fitting an equation such as the Schaefer model to a set of actual catch and effort data may be viewed as merely an interesting exercise unless one has to make actual management recommendations based upon the results. Then the situation becomes somewhat sticky. It is obvious that a simple deterministic model such as Schaefer's will not precisely describe the dynamics of a fish population. At best, there will be fluctuations in recruitment, growth, and catchability which will cause some consternation to the manager attempting to use such a model.

In the case of the shrimp fishery, the management strategy we propose treats the Schaefer model estimates as exactly correct, responds to indicated deviations from the optimum population size in a relatively arbitrary but conservative manner, and integrates the Oregon and California fishing. This conservative strategy attempts a gradual reduction in the biomass when the model estimates it to be above P_{opt} and a rapid increase in the stock size when it is estimated to be below P_{opt}. To formulate this procedure, let Q be the catch quota (California + Oregon) and $C_e(P) = HP^2 - KP$ be the equilibrium yield obtainable from a population of size P. With $P(t)$ the population when the next fishing season commences,

$$Q = \frac{P(t) - P_{opt}}{2} + C_e\left(\frac{P(t) + P_{opt}}{2}\right);$$

$$P(t) > P_{opt},$$

$$Q = P(t) - P_{opt} + C_e\Big(P(t)\Big);$$

$$P(t) < P_{opt}.$$

When the model predicts the stock is in the surplus condition we are, then, proposing to harvest one-half of this surplus plus the predicted sustainable yield at the point midway between $P(t)$ and P_{opt}. A predicted stock deficit evokes a procedure which harvests the sustainable yield at $P(t)$ minus the amount by which the stock falls short of P_{opt}. For example, the 1970 California shrimp quota of 3.4 million pounds was set by the above method with $P(t) - P_{opt} =$

7.1 — 4.8 = 2.3 and C_e (5.9) = 2.3 for a recommended yield of 3.4 million pounds (Table 1). It was assumed the Oregon fleet's catch from Oregon waters would be negligible.

A more radical strategy such as harvesting all of the surplus stock could be employed, but the attendant risks would be higher. These risks would include a possible disturbance of whatever stability exists in the population, particularly with reference to age structure. It might also be argued that the observed catch-per-effort should be used to adjust $P(t)$ before making the quota calculation described above. Here again, a substantial risk would be involved if the observed catch-per-effort were much higher than the expected since with our methods it could not be determined whether such an anomaly was due to abnormal catchability or to a real increase in the stock size. The quota-setting procedure we recommended above does respond in a limited way to a higher than expected catch. Since the fishery operates under a quota, a catch-per-effort which is higher than expected will result in the quota being filled with a lower than expected amount of effort and usually in a shorter time period. An examination of (2) shows that this will increase $P(t)$ and thus result in a larger quota for the season beginning at time t.

This fishery must be carefully followed in the future to observe how well the model based upon current parameters describes the observed catch and effort pattern. An equation such as this which is fitted to data from only 16 years cannot be considered definitive from a statistical estimation viewpoint and, in addition, there is a chance the population parameters will actually be changing. For example, one cannot avoid speculating about the effect of the large Pacific coast hake fishery on the shrimp natural mortality rate. Since hake may be a substantial predator upon shrimp (Gotshall, 1969), a reduction of the hake population due to a large fishery might increase the abundance of ocean shrimp.

Beyond the technical management problems which we have discussed at length, there is the institutional problem of a single state attempting to manage an interstate fishery. While the catch from Oregon waters by Oregon-based vessels has usually been so small that it affects the population negligibly, at times it has been substantial. A sustained change in conditions could nullify the effect of California's quota mechanism.

ACKNOWLEDGMENTS

Many biologists of the Department of Fish and Game collected the data used in this paper. Daniel W. Gotshall and Walter A. Dahlstrom were of special help to us in obtaining the data and in freely passing on to us their knowledge of this shrimp fishery and of shrimp life history. We also wish to thank Catherine L. Berude for programming and computing assistance.

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OBSERVATIONS ON SCALE PATTERNS AND GROWTH OF THE PACIFIC SARDINE REARED IN THE LABORATORY

MAKOTO KIMURA AND GARY T. SAKAGAWA[1]

ABSTRACT

Scale patterns and growth of Pacific sardine (*Sardinops caerulea*) were studied with laboratory-reared fish held for 24 months. All scales examined after the fourth month had accessory marks. The first accessory mark was formed in August to October and the second accessory mark, in May to August. The accessory marks were indistinguishable from annuli that formed in November to March.

Five possible causal factors of mark formation were investigated—temperature, salinity, gonad index, condition factor, and relative growth rate. Growth rate showed the best correlation. The accessory mark was formed during a period of change in growth rate and the annulus during a period of relatively constant growth rate.

An estimate of the body length-scale radius relation indicated that scales first increase in size at a body length of 33 mm.

Growth in length was rapid from the start of the experiment to the fourth month, after which the increase was gradual. The average instantaneous rate of growth was about 0.47/month during the first 4 months and about 0.03/month thereafter.

It was concluded that the abrupt increase in L_1 that was recorded in the 1940's for the sardine population was probably caused by errors in aging, owing to a change in scale readers and scale-reading criteria. The ages of fish age II and older were probably underestimated by the recent scale readers.

In the course of aging Pacific sardine (*Sardinops caerulea*) from scales, the senior author observed, from comparison of back-calculated lengths with growth curves, that accessory marks or false annuli occurred frequently and were easily mistaken for true annuli. This was contrary to the findings of Walford and Mosher (1943:8-9), who reported that the annulus was "present on all normal scales of an individual" whereas an accessory mark was only rarely present on "all the scales of an individual." Since misidentifying an accessory mark as an annulus can affect the estimated age of a fish, a laboratory experiment was conducted to determine (1) the frequency of occurrence of accessory marks, (2) the time of accessory mark formation, (3) possible factors that may cause accessory mark formation, (4) the time of annulus formation, and (5) the seasonal pattern of sardine growth. The experiment was initiated in May and was terminated approximately 24 months later. Results from the first 12 months of the experiment were reported by Kimura (1970), who showed that an accessory mark was present on scales of 4.5- to 5.0-month-old fish. This report is a more comprehensive presentation of results from the entire experiment.

METHODS

REARING

The collection of sardine eggs and the hatching and rearing of the young in the laboratory for the first 12 months were described by Kimura (1970). The general procedures, including those used after the 12th month, are briefly reviewed as follows. In May 1968, sardine larvae were hatched from eggs collected in plankton tows off San Diego, Calif., and the larvae were held in a

[1] National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

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polyethylene bag, which was suspended in a 4.6-m diameter pool (13.2 kliter). The pool also contained about 15 northern anchovy (*Engraulis mordax*) larvae. A 1,500-w mercury lamp that was suspended about 1 m above the bag provided illumination and a source of heat. The larvae were fed daily with plankton collected in Mission Bay, Calif., and live *Artemia*. On the 29th day the larvae were released into the pool. Feeding continued with plankton and live *Artemia* up to the 45th day, after which frozen *Artemia* and dry trout food were substituted. The daily ration was about 10% of the estimated total weight of fish alive on a given day, based on the average weight of fish sampled in the previous month.

On the 31st day the density of sardine larvae was noticeably reduced. Since few dead larvae were found during the previous days, the anchovies (average length 66 mm) were suspected of feeding on the sardines (average length 24 mm). Analysis of stomach contents of three anchovies revealed that they were indeed feeding on the sardines.[2]

During the first few months of the experiment, water was added to the pool only periodically to remove surface scum. But beginning on the 61st day, seawater was circulated continuously through the pool at an initial rate of about 19 liter/min. This rate was increased on the 180th day to about 34 liter/min.

SAMPLING

Fish were sampled and sacrificed at various intervals during most of the duration of the experiment. About 7-17 larvae were sampled daily from the polyethylene bag during the first month. During the second month 6-26 larvae were sampled primarily on a weekly basis. Starting with the third month and continuing through the 12th month, about 20-24 fish/month were sampled. After the 12th month, the sampling rate was reduced to 11-14 fish/month until an unusually large mortality from unknown causes reduced the population to 12 fish in the 16th month. Two more samples were taken thereafter; in one sample four fish were measured for length and returned to the pool. After the 24th month, the seven surviving fish were sampled and the experiment was terminated.

Standard length, total weight, gonad weight, and six scales removed from the body area at the tip of the pectoral fin (see Walford and Mosher, 1943:4) were obtained from most samples.

Water temperature was recorded daily on a thermograph. The monthly mean temperature ranged from 15.3° to 25.0°C and was generally 2.9°C higher than the monthly mean surface temperature recorded off the Scripps pier, La Jolla (Kimura, 1970), site of the water intake for the experimental pool[3] (see Lasker and Vlymen, 1969).

Salinity measurements were made by daily titrations from surface water sampled off Scripps pier. The mean values ranged from 33.09 to 34.38‰. It was assumed that water salinity was the same off the Scripps pier and in the experimental pool.

SCALE MEASUREMENTS

Scales were placed between two glass slides and viewed on a scale projector that magnified them 30 times. All marks that appeared to be annuli were recorded and the widths from focus to mark and focus to margin in the anterior field were measured.

ANALYSIS

Gonad weight was expressed as a percentage of total weight. This was designated a gonad index, or relative measure of sexual development.

The relative "fatness" of a fish was estimated

[2] To our knowledge there have not been previous reports on predation of sardine larvae by anchovies. The significance of our observation is that predation by anchovies may have contributed to the decline of the Pacific sardine population. Our anchovies were hatched from eggs and were 44 days older than the sardines. This difference in age (size) between the species is also found in the wild; the northern anchovy has a peak spawning period during January-March and the sardine, during April-June (Ahlstrom, 1966). The young of both species coexist in the California Current; thus it is conceivable that predation by anchovies is an important source of sardine natural mortality.

[3] The experimental pool was located at the Southwest Fisheries Center, about 1 km from the Scripps pier.

TABLE 1.—Results of aging of 205 known age, laboratory-reared sardines from scales.

Age (months)	Total number of fish	Total number of marks	Actual		Estimated				Percent disagreement
			Number with:		Number with:				
			0 mark	1 mark	0 mark	1 mark	2 marks	3 marks	
5	20	1	20	0	20	0	0	0	0
6	20	1	20	0	20	0	0	0	0
10	15	2	0	15	0	12	3	0	20.0
11	21	2	0	21	0	10	11	0	52.4
12	24	2	0	24	0	18	6	0	25.0
13	11	3	0	11	0	3	8	0	72.7
14	12	3	0	12	0	2	6	4	83.3
15	14	3	0	14	0	0	12	2	100.0
16	64	3	0	64	0	4	50	10	93.7
18	4	3	0	4	0	0	3	1	100.0

TABLE 2.—Frequency and percent (in parentheses) of Pacific sardines with various number of scale marks, as determined from scale reading. (Sardines were reared in the laboratory for 24 months.)

Age (months)	Number of fish	No mark	Accessory mark I	Annulus I	Accessory mark II	Annulus II
1	3	3 (100)				
2	8	8 (100)				
3	17	17 (100)				
4	9	4 (44)	5 (56)			
5	20		20 (100)			
6	20		20 (100)			
7	20		20 (100)	10 (50)		
8	20		20 (100)	13 (65)		
9	20		20 (100)	18 (90)		
10	20		20 (100)	20 (100)		
11	21		21 (100)	21 (100)		
12	24		24 (100)	24 (100)		
13	11		11 (100)	11 (100)	4 (40)	
14	12		12 (100)	12 (100)	6 (60)	
15	14		14 (100)	14 (100)	10 (100)	
16	64		64 (100)	64 (100)	64 (100)	
18	4		4 (100)	4 (100)	4 (100)	
24	7		7 (100)	7 (100)	7 (100)	7 (100)

by a condition factor (MacGregor, 1959). The factor (K) is calculated as a ratio of the weight in grams (W) to the cubic power of length in millimeters (L): $K = (W/L^3) \times 10^7$.

Back-calculated lengths from scale measurements were derived by two methods. Method one was by direct proportion, $L_m = (s_m/s_r)L$, where L_m = back-calculated length at time of mark (m) formation, s_m = scale width from focus to mark m, s_r = scale width from focus to margin, and L = length at sampling. Method two was also by direct proportion but with a correction factor (c) for body length when scales first increase in size in the Pacific sardine. The method uses the equation $L_m = c + (s_m/s_r)\ (L - c)$.

ACCESSORY MARKS AND ANNULI

FREQUENCY OF OCCURRENCE

An annulus is generally believed to form at annual intervals, usually as the result of a slowing down in growth such as occurs in winter for temperate species. An accessory mark, on the other hand, is believed to occur, if at all, at irregular intervals (Walford and Moser, 1943), the causes of which are unknown.

We examined the scales of the laboratory-reared fish and were unable to distinguish between the two types of marks. To test if other scale readers similarly could not distinguish accessory marks from annuli as we did, a series of scales from the laboratory-reared fish was mixed

with scales collected from wild fish and three experienced scale readers read the scales (Table 1). The percent error was as large as 100%, which indicates that accessory marks can indeed be easily misidentified as annuli.

TIME OF FORMATION

As many as four marks were observed on some scales. The percentage of fish with various numbers of marks was tabulated for each sample (Table 2). The results show that the first mark was formed from August to October (4-5 months old), the second from November to March (6-10 months old), the third from May to August (13-15 months old), and the fourth sometime after November (18 months old) but probably before January (20 months old). This January date for the fourth mark was deduced from two scales collected in late December from the bottom of the pool, but the data are not given in Table 2. The two scales had four distinct marks, but it is not known whether the scales were from one or two fish. The bottom of the pool was cleaned daily.

Based on the above criteria of an annulus and accessory mark, the second and fourth marks are annuli, and the first and third marks are accessory marks. The interval between annuli was about 12 months, and that between accessory marks was only 9 months.

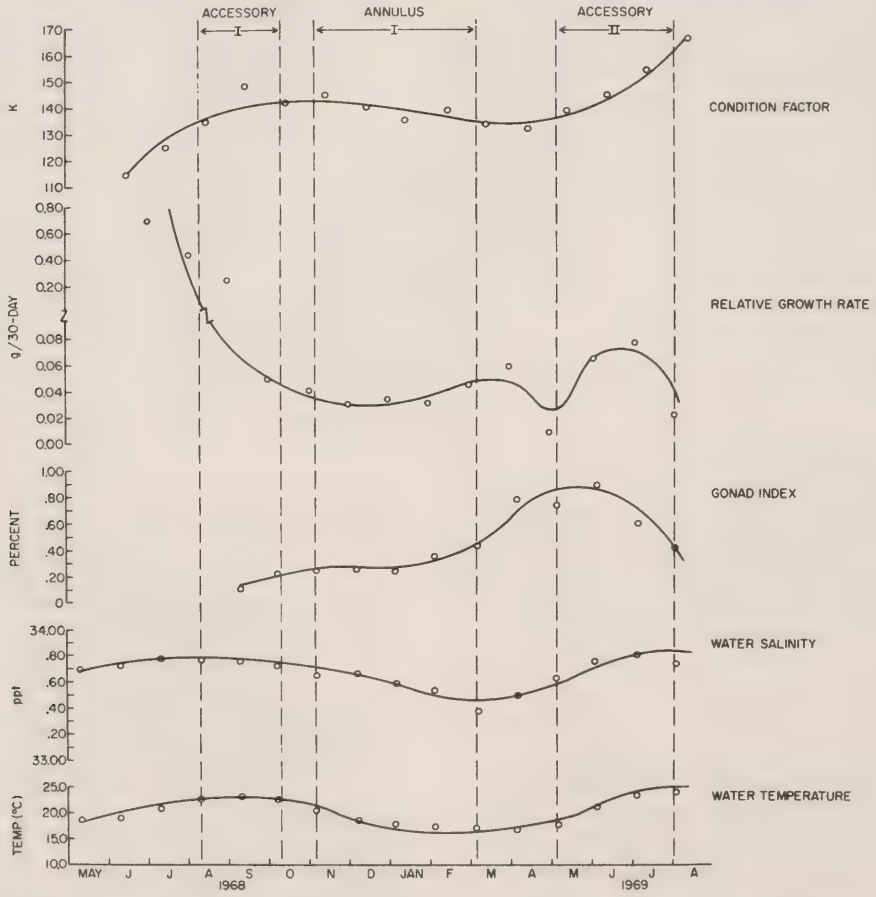

FIGURE 1.—Four possible factors that may be associated with mark formation on scales of Pacific sardines. Periods of mark formation are delineated by vertical lines.

POSSIBLE FACTORS AFFECTING MARK FORMATION

Water temperature and salinity, gonad index, condition factor, and growth rate were analyzed to determine whether they affected mark formation (Figure 1). Growth rate appeared to be best correlated with mark formation.

Kimura (1970) used monthly growth increments[4] for the first year to show that formation of the accessory mark was associated with maximum growth, and formation of the annulus was associated with the onset of rapid growth. His choice of growth increments for his analysis was not ideal because the magnitude of an increment is dependent on the size of the fish. We therefore chose to use the instantaneous rate of growth, $g = (\ln L_t - \ln L_0)/(t - t_0)$, Ricker (1958) on a 30-day basis to analyze the data from the entire experiment. The results (Figure 1) show that the accessory marks formed during periods of change in growth rate, whereas the annulus formed during a period of relatively constant growth rate.

GROWTH

BODY LENGTH-SCALE RADIUS RELATION

A body length-scale radius relation was fitted by least squares to data from 283 fish. A straight line of the form $Y = 32.856 + 9.030X$, where Y = standard length and X = scale radius, was calculated (Figure 2). The intercept of the line, or 32.856, is an estimated body length when scales first increase in size in the Pacific sardine. This estimate is probably too high, because scales with several circuli were observed on 26- to 30-mm long fish.

Landa (1953) reported 12 positive intercept values (68-191 mm) and 1 negative value (—102 mm) for body length-scale radius relations of fish caught by the commercial fishery in the 1940's. Compared to our estimate, his estimates are considerably larger. One reason for the difference is Landa used data from large fish (mean lengths of 186-228 mm), whereas we used data from small fish (mean length of 115 mm). This suggests that a relation over the entire size range of sardines may be nonlinear, although it is linear over a short segment of the curve. The parameters of a linear relation could hence vary, depending on the segment of the curve being examined.

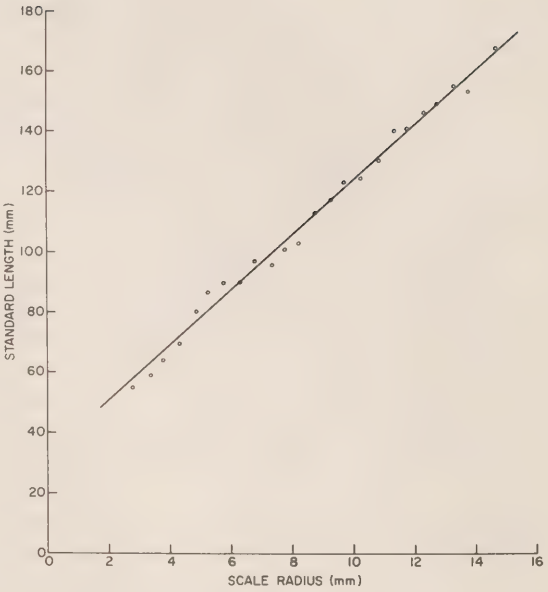

FIGURE 2.—Body length-scale radius relation for 283 laboratory-reared Pacific sardines.

WEIGHT-LENGTH RELATION

Data from 326 fish were used to estimate the weight-length relation. The relation (Figure 3) appears to underestimate the average weight of fish greater than 135 mm long. This is probably because the weight-length relation was based on data from individual fish whereas the data points in Figure 3 represent average weights for 5-mm groupings of lengths.

Clark (1928) estimated a weight-length relation for sardines landed at San Pedro, Calif., in the 1920's. Her estimate was compared to ours

[4] In Kimura's Figure 3 the notations for weight and length increments are mislabeled. The increments are not percentages but absolute values.

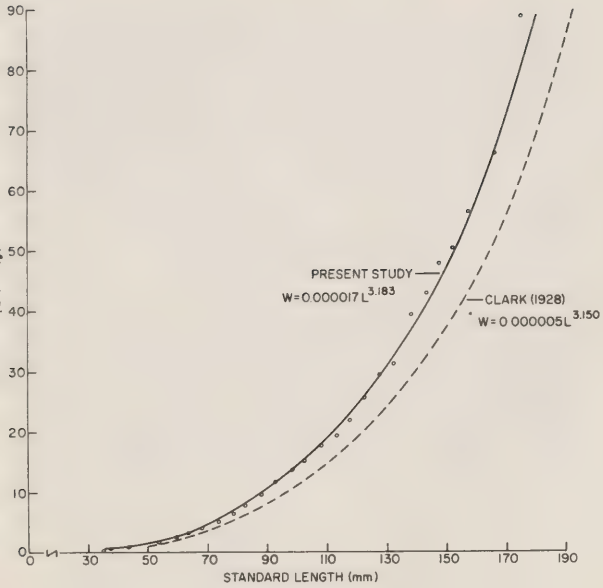

FIGURE 3.—Weight-length relation for the Pacific sardine.

(Figure 3) and found to be significantly different based on analysis of covariance ($F = 18.02$, df = 1, 237). The laboratory-reared fish were appreciably heavier for a given length than sardines caught in the 1920's. This may be attributed to several causes, among them difference in diet, in amount of exercise, and in the range of sizes sampled.

SEASONAL GROWTH PATTERN

Growth of the Pacific sardine has been well documented by several investigators (e.g., Walford and Mosher, 1943; Phillips, 1948; Felin, 1954; Clark and Marr, 1955). Most of the studies have concentrated on estimating growth based on scale readings of fish caught by the commercial fishery.

Another method of estimating growth is by rearing experiments. Although we recognize the limitation of laboratory vs. natural conditions, we believe that estimates of growth of laboratory-reared sardines can indicate the general trend in growth in the wild. We therefore estimated growth of our laboratory-reared sardines.

As shown in Figure 4, growth in length was rapid from the start of the experiment to the fourth month, after which the increase was more gradual. The average instantaneous rate of growth was about 0.47/month during the first 4 months and about 0.03/month during the fifth to 24th month. In contrast, growth in weight increased somewhat exponentially during two phases: during the first 4 months and again during the fifth to 14th month (Figure 5).

Walford and Mosher (1943) reported the standard lengths of juvenile sardines caught in monthly samples in the late 1930's. Although the date of birth, and hence the exact age, of

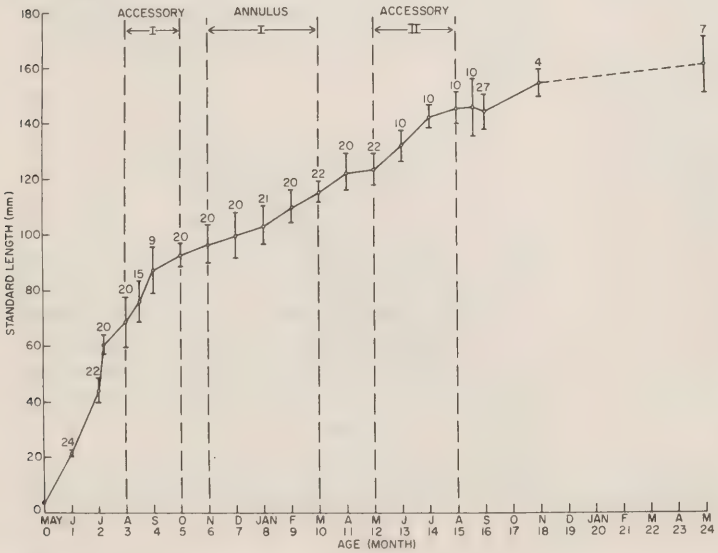

FIGURE 4.—Growth in length of Pacific sardines reared in the laboratory for 24 months. Mean length is represented by a circle, and one standard deviation is shown on each side of the mean. The sample size is also indicated. The first accessory mark occurred in August-October, and the second in May-August. The first annulus formed in November-March, and the second apparently in December.

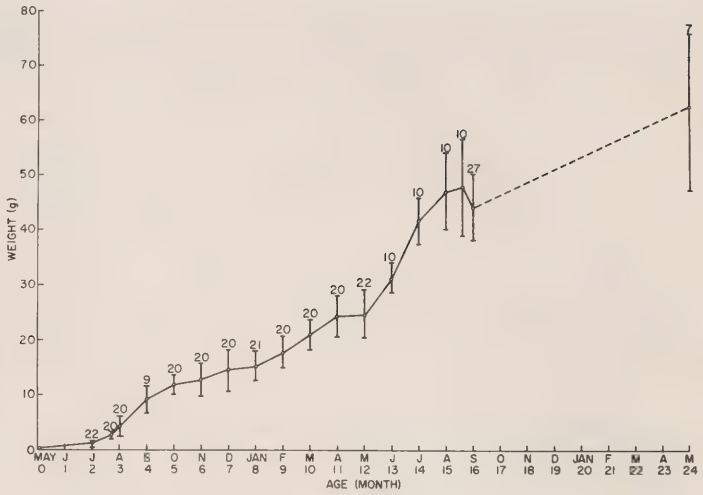

FIGURE 5.—Growth in weight of Pacific sardines reared in the laboratory for 24 months. Mean weight is represented by a circle, and one standard deviation is shown on each side of the mean. The sample size is also indicated.

their fish was not known, we compared their data for the 1937 and 1938 year classes with ours (Figure 6). The results indicate that although growth of the 1937 year class was fast, growth was similar in fish caught in the 1930's and in the laboratory-reared fish.

Marr (1960) presented data on the average length at time of first annulus formation (L_1) and showed that there was a sharp change in L_1 to a higher level with the 1944 year class landed at San Pedro. Using his data, we calculated separate estimates of average L_1: one for the 1934-43 year classes, and another for the 1944-57 year classes. The estimates are 101.3 and 131.5 mm, respectively. Compared with our estimate of 103.0 mm, growth of the 1934-43 year classes was almost identical to that for the laboratory fish, and growth for the 1944-57 year classes appears to have been faster than that for the laboratory fish. This faster growth may be an artifact and is discussed in a later section.

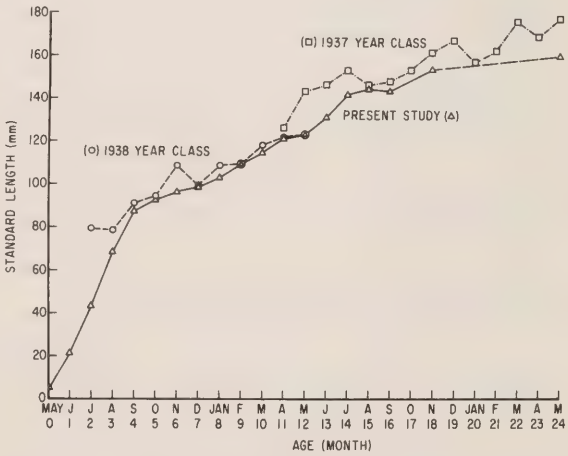

FIGURE 6.—Comparison of growth of juvenile sardines caught in the 1930's with growth of laboratory-reared sardines. Data for the 1937 and 1938 year classes are from Walford and Mosher (1943).

BACK-CALCULATED LENGTHS

Back-calculated lengths were computed for two samples, taken in September (16th month) and May (24th month). We reasoned that the back-calculated lengths would give an independent estimate of the time of mark formation, if growth is assumed to follow that shown in Figure 4. The average back-calculated lengths based on two methods are shown in Table 3. The first method gave lower estimates than the second. Both methods, however, gave back-calculated lengths that were reasonably similar to average lengths of samples collected during the period when the marks formed.

TABLE 3.—Back-calculated length of sardines sampled on two dates. The two methods of back-calculating length are discussed in detail in the text; in general, method 1 is by direct proportion, and method 2 is by direct proportion with a correction factor for the body length-scale radius relation.

Sampling date	Method	Average length (mm) at:					Sample size
		Accessory mark I	Annulus I	Accessory Mark II	Annulus II	Margin	
September	1	71.5	99.9	135.6	--	143.3	27
	2	88.9	110.6	137.8	--	143.3	27
May	1	75.1	104.7	137.4	153.1	160.3	7
	2	93.6	116.8	142.3	155.0	160.3	7

DISCUSSION

MARK FORMATION ON SCALES

Walford and Mosher (1943) indicated that on sardine scales an accessory mark was distinguishable from an annulus by its finer sculpturing and its rare occurrence on all scales of an individual. The results of our study on sardines reared in the laboratory showed that accessory marks occurred on all scales examined after the fourth month, and they were generally indistinguishable from annuli. But for some scales in which the accessory mark was distinguishable from an annulus, the identifiable characteristic was the fine sculpturing mentioned by Walford and Mosher.

Interruptions in the growth pattern are generally assumed to form marks on scales (e.g., see Van Oosten, 1957). It is also widely assumed that the driving mechanism behind mark formation is temperature, through the influence of a fish's metabolism (Brown, 1957). Our results indicate that mark formation is unrelated to temperature, but appears to be related to growth rate. Hogman (1968) obtained somewhat similar results in his experiments with coregonids. He found that formation of marks was closely related to growth and somewhat related to temperature. However, Hogman indicated that light period may be the primary driving mechanism. Bilton and Robins (1971) found that mark formation was correlated with increase in food supply, but not with resumption of feeding after starvation in sockeye salmon. Their experiments with light period proved inconclusive. It thus appears that mark formation in fishes is probably related to growth, although the actual driving mechanism(s) have so far not been clearly identified.

ERROR IN AGING

Scales are routinely used to age and study growth of the Pacific sardine. Our results indicate that extreme caution must be exercised in aging because of the presence of accessory marks on scales. Furthermore, since the annulus is formed during the winter, the actual age of a fish at time of first annulus formation may vary depending on its date of hatching. In our study the first annulus was laid down after the sixth month for fish hatched in May. May is the middle of the heavy spawning season for the Pacific sardine, but the season extends from March to October (Kramer and Smith, 1971).

Kimura (1970)[5] conducted an experiment to test the consistency of early and recent scale readers in aging sardines from scales. He found that the abrupt increase in L_1, as reportedly observed in the 1940's by Marr (1960) for sardines landed at San Pedro, may have actually been caused by a change in scale readers and in criteria used in reading scales. We compared our average length at annulus formation with the average L_1 of fish aged by the early ($L_1 = 101.3$ mm) and recent ($L_1 = 131.5$ mm) scale readers, and discovered that the early readers probably aged sardines correctly, whereas the recent readers probably underestimated the age of age II

[5] Kimura, M. 1970. Possible errors in locating the first scale annulus and in estimating the length of Pacific sardines. Manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, CA 92037.

and older fish. If this was the case, and assuming that growth has not appreciably changed, then the number of fish that was incorrectly aged as age I by recent scale readers was at most equal to the number of fish correctly aged as age I. This is deduced from the fact that the presumably overestimated L_1 of 131.5 mm is about midway between our L_1 of 103 mm and L_2 (=length at time of second annulus formation) of about 160 mm.

Back-calculated lengths for Pacific sardines (Marr, 1960) have been based on Method 1. A statistical test of the intercept of our body length-scale radius relation (Figure 2) indicated that the intercept is not significantly different from zero ($t = 1.831$, df $= 282$). Although this indicates that Method 1 is acceptable, the back-calculated lengths at first annulus are appreciably and significantly different between Method 1 and Method 2 (Table 3). It is therefore advisable that Method 2 be used since it is the better procedure (Ricker, 1969).

We conclude from these results that a bias may be present in published accounts of the age composition of the Pacific sardine catch, which in turn may have affected studies on the population dynamics of the Pacific sardine. We recommend that the method of aging Pacific sardines be reevaluated, perhaps with the consideration of modifying the scale method so that the scale reader is made aware of the length of fish being aged or even utilizing other hard parts for aging, and that appropriate steps be taken to eliminate aging errors in the historic records on age composition of the catch. We realize that this task will not be easy, but it may be worthwhile because of the frequent use of the records to analyze fisheries hypotheses.

ACKNOWLEDGMENTS

We thank C. E. Blunt, Jr., J. E. Hardwick, and J. S. MacGregor for participating in our test to determine whether accessory marks can be misidentified as annuli. P. Paloma and A. Saraspe assisted in hatching and rearing the sardines. D. Kramer, W. H. Lenarz, J. S. MacGregor, and A. M. Vrooman kindly reviewed the manuscript and gave helpful suggestions. J. R. Thrailkill drew the figures. We are indebted to these individuals.

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UNSTRUCTURED MARINE FOOD WEBS AND "POLLUTANT ANALOGUES"

JOHN D. ISAACS[1]

ABSTRACT

The several species of fish living in the Gulf of California have been shown to possess quite different concentrations of cesium (and cesium in respect to potassium) than the same species of fish living in the Salton Sea. The Salton Sea fish display simple trophic steps of concentration, whereas those in the Gulf all show about the same levels. These differences are reasonably well explained by simplified trophic models of the two environments. The concentration factor found in the known and describable *food chain* of the Salton Sea, applied to a model of an assumed unstructured *food web* in the Gulf, leads to reasonable results. This suggests that study of the concentrations in marine organisms of such natural trace substances as cesium may lead to an understanding of the trophic position of the organisms, and hence constitute "pollutant analogues" that may yield a better understanding of the existing or potential distribution of pollutants in marine organisms.

Young (1970) found that the cesium content of the muscle of the several species of fish in the Salton Sea (California) increased by about a factor of 2 (average 2.15) in each of the successive steps in the simple linear food chain existing in that isolated marine environment and that the cesium/potassium (Cs/K) ratio similarly increased by about a factor of 3 (average 3.1). Results both for normal and radioactive cesium were in agreement. Young further demonstrated that the entry of the cesium into the food chain was via the phytoplankton, only. However, Young found that the same several species of fish in the Gulf of California displayed no such successive steps of increase, but rather, that the muscle tissue of all contained about the same concentration of cesium (with the supposedly more primary feeding mullets surprisingly having a somewhat greater than average concentration of cesium). Young's results are summarized in Table 1, where it can be seen that the Cs/K ratio is elevated by about a factor of 16 between the primary food and the fish in the Gulf of California.

Young suggested that these differences might be the result of a complex food web in the Gulf of California, and reported some evidence for this in the stomach contents of these Gulf fish.

DEVELOPMENT OF AN UNSTRUCTURED FOOD WEB MATRIX AND EQUATIONS

The following is an attempt to develop a highly simplified model of a generalized food web, to discuss some of its implications, and to test its validity by using real data.

Let us first assume that in a food web each transfer of organic material (or energy), or of individual elements such as cesium, from one component of the web to another can be characterized by the following quantities:

K_1 = a coefficient of conversion of matter (or energy) in food into living tissue

K_2 = a coefficient of conversion of matter (or energy) in food into irretrievable form (e.g., by respiratory combustion or mineralization)

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TABLE 1.—Summary of Young's results.

Item	Salton Sea			Gulf of California	
	Cs/K ratio × 10^6	Concentration factor relative to food		Cs/K ratio × 10^6	Concentration factor relative to food
Water	3.5 ± 0.1			0.823 ± 0.047	
Algae	4.0 ± 1.0			[1] 0.823 ± 0.047	
Invertebrate[2]	3.8 ± 8.5	1.0 — 2.1			
Mullet	9.0 ± 1.1	2.3 ± 0.7	(algae)	15.2 ± 1.7	18.5 ± 2.0
Shad	14.8 ± 3.1	2.7 ± 0.7	(invertebr.)[2]		
Sargo-croaker	26.0 ± 2.7	5.5	(invertebr.)[2]	13.2 ± 1.0	16.0 ± 1.2
Corvina	57.7 ± 7.7	2.0 ± 0.3	(croaker)	10.4 ± 0.8	12.7 ± 1.0
	Average	3.1 ± 0.8		12.8 ± 1.1	15.6 ± 1.3

[1] Cs/K for algae taken as Cs/K for water.
[2] Concentration factor involves values for specific invertebrates within the range shown.

K_3 = a coefficient of conversion of matter (or energy) in food into nonliving but retrievable form (e.g., organic detritus or dissolved organic matter)

For each component

$$K_1 + K_2 + K_3 = 1 \qquad (1)$$

$0 < K_i < 1$, where $i = 1, 2$, or 3.

These coefficients are assumed to apply to the nutrient processes of all heterotrophs in the system, microorganisms, invertebrates, and vertebrates alike. Further they are assumed to have constant mean values for each ingested component of a food web in which plant production is the only primary source.

Under these assumptions, some of the principal characteristics of a generalized food web can be represented by a matrix such as Figure 1. Each division along an abscissa represents the conversion of a fraction, K_1, of any arbitrary unit of food into living tissue. Therefore, the numbers on the horizontal axis are powers of K_1. Each division along an ordinate similarly represents the conversion of a fraction, K_3, of any arbitrary unit of food into retrievable but nonliving organic matter, and the numbers on the vertical axis are, thus, powers of K_3. These numbers can be used to name points in the matrix as in any set of cartesian coordinates. One use of the matrix can be illustrated by considering a unit of food, M_m, (e.g., in a copepod or in an edible nonliving particle) at 2, 3. If it is consumed by a heterotroph, the fraction K_1 is converted into tissue and the fraction K_3 into nonliving retrievable matter. The sum of these two fractions M_m $(K_1 + K_3)$ is now found at 3, 4. Its trajectory in the matrix is always to the right and down.[3] All points on a line at right angles to this trajectory (e.g., a diagonal line) can be considered to represent organic matter that has undergone the same number of steps of conversion from its origin as tissue of autotrophic organisms. The expression at the end of each diagonal line in Figure 1 is the sum of all fractions of an original unit of organic matter along that diagonal.

The number of possible paths from the origin to each point in the matrix is easily counted and is the sum of the two numbers of units shown at the point, the lower right-hand number being the number of paths resulting in living matter (or energy) at that point, and the upper left-hand number being the number of paths resulting in nonliving but recoverable matter (or energy) at the point.

It will be seen that this doubly infinite matrix is composed of two superimposed binomial (Pascal) triangles, and can be summed along diagonals resulting in two infinite series of binomials of the form:

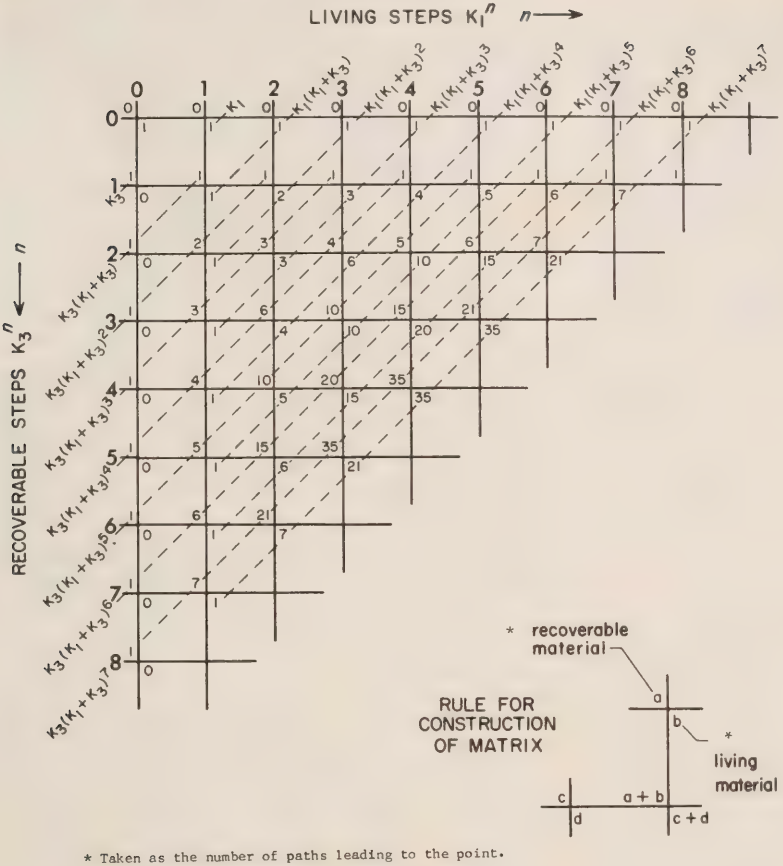
$$a + a(a + b) + a(a + b)^2 + a(a + b)^3 \ldots a(a + b)^n.$$

The sum of such a series is

$$\frac{a}{1-(a+b)} \qquad (2)$$

and for the sum of living matter (or energy),

[3] Cases may be considered in which either K_1 or $K_3 = 0$ and motion is either only to the right or only down. $K_1 = 0$ is, of course, not a permanently viable condition.



* Taken as the number of paths leading to the point.

FIGURE 1.—Matrix representing principal characteristics of a generalized food web.

$a = K_1$, $b = K_3$, and for the sum of recoverable matter (or energy), $a = K_3$, $b = K_1$.

These series can be further modified and summed in several ways. We will define a term, M_0, where M_0 is an increment of initial input periodically introduced into the system at intervals equal to the time taken by one average step in the food web. Under the assumption that all steps are equally probable, the diagonals along which the matrix has been summed mark equal intervals of time. Thus, allowing the quantity M_0 to be successively introduced at the origin of the matrix, the total quantity of material in the entire web, above the phytoplankton level, (M_t) for steady state becomes:

$$M_t = M_t' + M_t'' \qquad (3)$$

where M_t' = total in living material, and

M_t'' = total in nonliving recoverable material;

$$M_t' = M_0 \frac{K_1}{1-(K_1+K_3)} = \frac{M_0 K_1}{K_2} \qquad (4)$$

$$M_t'' = M_0 \frac{K_3}{1-(K_1+K_3)} = \frac{M_0 K_3}{K_2} \qquad (5)$$

$$M_t = \frac{M_0(K_1+K_3)}{K_2} \,. \qquad (6)$$

FURTHER VARIATIONS OF THE FOOD WEB MATRIX ANALYSIS

Later I will delete earlier steps in the matrix series. In this case, a more general solution of equation (4) involves a summation of the matrix above any step. Here the partial sum,

$$M_p' = \frac{M_0 K_1 (K_1 + K_3)^p}{1 - (K_1 + K_3)} \quad (7)$$

where p is the number of steps of the series eliminated.

Other types of formulations and summations are, of course, possible. For example, differences in the time for living-to-living and recoverable-to-living steps may be incorporated by multiplying the constant appropriate to the slower step by another constant representing the inverse ratio of the times of the two respective processes.

As another example, the average content of each *point* in time in the matrix can be derived by dividing each term of the series by the number of points along the particular diagonal.

Other manipulations of this matrix will be suggested later.

CALCULATION OF THE COEFFICIENTS OF THE PREDACEOUS FOOD WEB

For the purpose of examining Young's results on cesium, we will proceed with equations (4), (5), and (7) and test the hypothesis that the carnivorous fishes of the Gulf of California are members of an unstructured food web. That is to say that they randomly draw from the mean composition of the food web above the plant level.

Since, from the Salton Sea results, the Cs/K ratio increases by a factor of about 3 for each living step, we can say that

$$K_{1c} \cong 3K_{1f}, \text{ for organic food material} \quad (8)$$

and since the invertebrates in the Salton Sea which feed partially on detritus show no substantially different increase in Cs/K ratio, I will assume that a double step from living to recoverable to living material also results in an increase in the Cs/K ratio of only about 3, and, hence, that

$$K_{3c} \cong K_{3f} \quad (9)$$

where subscript c denotes the coefficients K_1 and K_3 applicable to the Cs/K ratio, and subscript f those applicable to food.

For the conditions in the Gulf of California, it is clear that, with the exception of the mullet, the fish do not consume plant material directly, and we can eliminate the first step in the series, and thus, for non-herbivorous omnivores, $p = 1$, and equation (7) becomes

$$M_p = M_0 \frac{K_1 (K_1 + K_3)}{1 - (K_1 + K_3)}. \quad (10)$$

Let us also define the Cs/K ratio in the plant material as:

$$q_c = \frac{M_{oc}}{M_{of}}$$

$$\text{then } \frac{M_{pc}}{M_{pf}} = \frac{q_c \dfrac{K_{1c}(K_{1c} + K_{3c})}{1 - (K_{1c} + K_{3c})}}{\dfrac{K_{1f}(K_{1f} + K_{3f})}{1 - (K_{1f} + K_{3f})}} = 16 q_c \quad (11)$$

where the coefficient 16 is approximately the mean increase in the Cs/K ratio from algae to predaceous fish in the Gulf (Table 1), and subscripts are as in equations (8) and (9).

Substituting (8) and (9), equation (11) *for food*[3] becomes

$$39K_1^2 + K_1(52K_3 - 7) - 13K_3(1 - K_3) = 0. \quad (12)$$

Assumption of a range of reasonable values of K_3 results in the following:

K_3	K_1	M_t'/M_0	M_t''/M_0	M_t'/M_t''
0.0	0.18	0.22	0.0	--
0.1	0.20	0.29	0.14	2.10
0.2	0.19	0.31	0.33	0.94
0.3	0.18	0.35	0.58	0.60
0.4	0.16	0.36	0.91	0.40

Values of ratios M_t'/M_0 (living material to input), M_t''/M_0 (recoverable to input) and M_t'/M_t'' (living to recoverable) are derived, but it is not known what values of these ratios might exist in nature.

The values of K_1, however, are within the range of values of conversion commonly found in laboratory experiments and culture operations involving growing animal populations.

We can thus conclude that the assumption of

[3] In the remainder of this paper, $K_1 \equiv K_{1f}$, and $K_3 \equiv K_{3f}$.

an unstructured food web in the Gulf of California in explanation of Young's findings on *predaceous* fish leads to reasonable estimates of the coefficient of conversion of food.

PELAGIC VERSUS SHALLOW WATER POPULATIONS

Other variations or testable conclusions or manipulations of these equations can be undertaken. For example, we can derive the relative biomass of two similar environments where, in one, the recoverable matter approaches zero. These might be a near-surface population over deep water where $K_3 \rightarrow 0$ because of rapid sinking of inert particles compared with a similar population over shallow water where K_3 could have any of the values shown in the table above.

From equation (4)

$$\frac{M_t' \text{ pelagic}}{M_t' \text{ shallow}} = \frac{M_0 \text{ pelagic}}{M_0 \text{ shallow}} \times \left(1 - \frac{K_3}{1-K_1}\right). \quad (13)$$

For the range of values found in the Gulf

$K_3 = 0.0$	$K_1 = 0.18$	$(1-\frac{K_3}{1-K_1})$	$= 1.00$
$K_3 = 0.1$	$K_1 = 0.20$	"	$= 0.88$
$K_3 = 0.2$	$K_1 = 0.19$	"	$= 0.75$
$K_3 = 0.3$	$K_1 = 0.18$	"	$= 0.62$
$K_3 = 0.4$	$K_1 = 0.16$	"	$= 0.52$

THE MULLET ANOMALY

The high Cs/K ratio of the mullet is difficult to explain. It is generally thought that the mullet is largely herbivorous. Three possible factors may give rise to the anomalous levels: First, the mullet in the Gulf of California may ingest far more organisms with the detrital material than is generally supposed, and these organisms may be part of a microscopic multistep food web that generates a high Cs/K ratio. No such effect was apparent in the Salton Sea, however, possibly because of the paucity and simplicity of invertebrate infauna in the detrital mat. Secondly, some members of the detrital community in the Gulf may take up inorganic cesium from the sediment, unlike those of the Salton Sea. Third, the high fat level of the mullet results in their possessing a caloric level, as related to organic material, that is 1.6 that of the other fish. This argues that it might be more significant to normalize cesium to calories than to dry organic weight, since more food intake (and hence more cesium) possibly is required for a given increment of growth in a fish with high fat content, with the potassium better normalized to fat free dry weight. This latter assumption would bring the Cs/K ratio in the mullet into the lower ranges of that in predaceous fish.

Pursuing this latter possibility, the adjusted Cs/K ratio for Gulf mullet can be set at about 10, and considering that the composition of the detrital feeding creatures (M_d) should be [from food represented by equation (5)]

$$M_d = M_0 \frac{K_1 K_3}{1-(K_1+K_3)}; \quad (14)$$

then the Cs/K ratio should be

$$\frac{M_{dc}}{M_{df}} = \frac{q_c \dfrac{K_{1c}K_{3c}}{1-(K_{1c}+K_{3c})}}{\dfrac{K_{1f}K_{3f}}{1-(K_{1f}+K_{3f})}} = 10q_c. \quad (15)$$

Substituting equations (8) and (9), as before, this becomes

$$K_3 = 1 - \frac{27}{7} K_1 \quad (16)$$

which is within the range of values for these constants previously derived (e.g., $K_3 = 0.30$, $K_1 = 0.18$). In simultaneous solutions of equations (12) and (16) values of K_3 are extremely sensitive to the values of concentration. The values of K_1, however, are essentially stable.

CONCENTRATION FACTORS

It should be noted in this discussion that the high concentration of cesium in the mullet may be a specific case of a more general principle, which is that the concentration factor (f_c) of a trace substance in a single step may be inversely

related to the coefficient of conversion of food (in terms of material). Certainly the upper value of f_c is limited to the total trace substance intake "diluted" by the new growth and hence,

$$f_c \not> \frac{1}{K_{1f}} \quad . \tag{17}$$[4]

This argues that a creature with a low coefficient of conversion for food can show high concentrations of trace elements or pollutants for this reason alone.

Such lower coefficients of conversion and high concentration of trace elements may result from definitive growth, sickness or abnormality or, as probably in the case of the mullet, when food is converted into a more energetic form. Conclusions as to cause and effect of pollutant trace element concentrations in creatures with abnormalities must thus be considered with caution.

CONCLUSIONS

The assumption and analysis of an unstructured food web is reasonably consistent with findings on the concentration of the element cesium (in respect to potassium) in the Gulf of California. It suggests that unstructured marine food webs may be common and that the distribution of natural trace elements, such as cesium, may give insight into food webs in general, and hence into the existing or potential distribution of pollutants.

ADDENDUM

Several reviewers of this paper have suggested that I expand the treatment of trophic types in an unstructured food web. Dominance of any highly complex trophic types is incompatible with an unstructured food web hypothesis. However, the following may be considered compatible (from equations 4, 6, or 7 as appropriate):

Strict herbivores

$$M_n = M_0 K_1 \tag{19}$$

Omnivores

$$M_v = M_0 \frac{K_1}{1 - (K_1 + K_3)} \tag{20}$$

Particle feeders
(detritus + phytoplankton)

$$M_u = M_0 \frac{K_1 (1 - K_1)}{1 - (K_1 + K_3)} \tag{21}$$

Detrital feeders

$$M_d = M_0 \frac{K_1 K_3}{1 - (K_1 + K_3)} \tag{14}$$

Feeders on the detrital
milieu (detritus and detrital feeders)

$$M_{d+t} = M_0 \frac{K_1 K_3 (1 + K_1)}{1 - (K_1 + K_3)} \tag{22}$$

Strict predators

$$M_p = M_0 \frac{K_1^2}{1 - (K_1 + K_3)} \tag{23}$$[5]

Non-herbivorous omnivores

$$M_v = M_0 \frac{K_1 (K_1 + K_3)}{1 - (K_1 + K_3)} \tag{10}$$

[4] This can be derived more formally as follows: let C_f be the concentration in the food; then

$$C_f = \frac{q_c}{q_f}$$

where q_c is quantity of the substance and q_f is total quantity of food material.

Then the concentration in the organism,

$$C_0 = \frac{q_c K_{1c}}{q_f K_{1f}} = C_f \times \frac{K_{1c}}{K_{1f}}$$

since

$$f_c = \frac{C_0}{C_f} = \frac{K_{1c}}{K_{1f}} \quad , \text{ and}$$

$K_{1c} \not> 1$, then

$$f_c \not> \frac{1}{K_{1f}} \quad .$$

[5] Equation 23 could well have been employed instead of equation (10) in the previous treatment. Differences in results would be small, however.

These expressions can be employed to generate expressions for the coefficient R, or the increase in the concentration of any component passing through the food web and introduced only via plants. The derivation follows that of equation (11) above, where j is the coefficient of increase over the conversion of food, as in equation (8) above, where $j \cong 3$. Also, for interest, is shown the coefficient N, which is the limiting or maximum increase in the biomass of each trophic type resulting from a unit input into the food web (i.e. $M_0 = 1$), evaluated from the above equations.

	R	Equation No.	R^*	N^*
Strict herbivores	j	(24)	3.0	0.18
Omnivores	$\frac{jK_2}{1 - jK_1 - K_3}$	(25)	9.7	0.35
Particle feeders	$\frac{jK_2\,(1 - jK_1)}{(1 - K_1)\,(1 - jK_1 - K_3)}$	(26)	5.5	0.28
Detrital feeders	$\frac{jK_2}{1 - jK_1 - K_3}$	(27)	9.7	0.10
Feeders on the detrital milieu	$\frac{jK_2\,(1 + jK_1)}{(1 + K_1)\,(1 - jK_1 - K_3)}$	(28)	12.7	0.12
Strict predators	$\frac{j^2K_2}{1 - jK_1 - K_3}$	(29)	10.4	0.06
Non-herbivorous omnivores	$\frac{jK_2\,(jK_1 + K_3)}{(K_1 + K_3)\,(1 - jK_1 - K_3)}$	(30)	15.0	0.17

* for $K_1 = 0.18$, $K_3 = 0.30$, $j = 3$

It should be noted that the coefficient N indicates only the potential increase of the biomass of each trophic type, as related to productivity input. The potential population (standing crop) depends upon how closely this maximum is approached, and the fecundity, mortality, etc. of the appropriate organisms.

It should also be noted that the usefulness of the total assumptions of this model can be tested by the determination of R for an appropriate trace element, such as Cs, in samples of well defined trophic types.

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IN MEMORIAM: OSCAR ELTON SETTE

Oscar Elton Sette died on July 25, 1972, at Palo Alto, Calif. He was 72. On September 7th his ashes were scattered at sea from the research vessel *David Starr Jordan.*

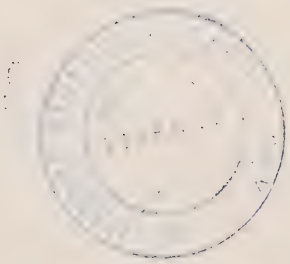
The last issue of this journal (*Fishery Bulletin*, Vol. 70, No. 3) was dedicated to Elton Sette. His colleagues who contributed papers to that thick number make up a roster of some of the most able scientists in the field of marine research today, yet it was woefully incomplete, because many who had wished to contribute were unable to do so. The number had been planned by his friends as a surprise gift to Elton (but how it would have benefited from his quick editorial eye!): it must now stand as a memorial.

Towards mid-July, Phil Roedel, Director of the National Marine Fisheries Service, wisely broke the 2 years of secrecy surrounding the "Sette number" and sent Elton the table of contents and a copy of Pat Powell's warm portrait. Elton was pleased.

Since July 1970, Elton had been a member of the Editorial Committee of the *Fishery Bulletin.* This is the first number not to carry his name. Assuredly, it will not be the last to show his influence on the course of marine research. We had planned a gift to him: he left one to us — a standard of high and unflagging professional competence. Not many men leave as much.

Reuben Lasker
Scientific Editor

Thomas A. Manar
Chief, Scientific Publications Staff



TEMPERATURE AND PHYTOPLANKTON GROWTH IN THE SEA

Richard W. Eppley[1]

ABSTRACT

The variation in growth rate with temperature of unicellular algae suggests that an equation can be written to describe the maximum expected growth rate for temperatures less than 40°C. Measured rates of phytoplankton growth in the sea and in lakes are reviewed and compared with maximum expected rates. The assimilation number (i.e., rate of photosynthetic carbon assimilation per weight of chlorophyll *a*) for phytoplankton photosynthesis is related to the growth rate and the carbon/chlorophyll *a* ratio in the phytoplankton. Since maximum expected growth rate can be estimated from temperature, the maximum expected assimilation number can also be estimated if the carbon/chlorophyll *a* ratio in the phytoplankton crop is known.

Many investigations of phytoplankton photosynthesis in the ocean have included measures of the assimilation number, while fewer data are available on growth rate. Assimilation numbers for Antarctic seas are low as would be expected from the low ambient temperatures. Tropical seas and temperate waters in summer often show low assimilation numbers as a result of low ambient nutrient concentrations. However, coastal estuaries with rapid nutrient regeneration processes show seasonal variations in the assimilation number with temperature which agree well with expectation.

The variation in maximum expected growth rate with temperature seems a logical starting point for modeling phytoplankton growth and photosynthesis in the sea.

Temperature does not seem to be very important in the production of phytoplankton in the sea. For example, Steemann Nielsen (1960) has written, "Recent investigations have shown, however, that the direct influence of temperature on organic production in the sea is fairly insignificant." Other reviewers of photosynthesis in the sea likewise give little or no consideration to a role of temperature and Steemann Nielsen's statements find widespread endorsement in the published data on geographic and seasonal variation in marine phytoplankton photosynthesis.

In response to this, the reader may ask at least two questions: (1) Why is temperature of so little importance and (2) why would anybody write a review on temperature and phytoplankton growth in the oceans? Several answers to the first question have appeared in the literature and some of these will be discussed in this account. I have two answers for the second question. The purpose of this review is (1) to suggest maximum growth and photosynthetic rates which might be reasonably expected for natural marine phytoplankton and (2) to point out the interrelationship among growth rate, photosynthetic assimilation number (i.e., rate/chlorophyll), and carbon/chlorophyll *a* ratios in the phytoplankton.

What follows is an attempt to show that temperature sets an upper limit on phytoplankton growth rate and on the rate of photosynthesis per weight of chlorophyll, and that this upper limit can be predicted from a knowledge of temperature and the carbon and chlorophyll content of the plants.

It can perhaps be inferred, from above, that phytoplankton growth in the oceans seldom approaches the upper limits imposed by the temperature of the water and that temperature does not figure prominently in simulation models for primary production in the marine environment. Other factors effect reduced rates of growth and

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photosynthesis and diminish the potential production of phytoplankton. Nevertheless, earlier reviewers have been able to generalize on several aspects of the relation between phytoplankton growth and temperature (see especially Talling, 1957; Steemann Nielsen, 1960; Ichimura and Aruga, 1964; Yentsch and Lee, 1966; Ichimura, 1968). Culture experiments have revealed that clones of a species isolated from cold or warm seas may differ in their optimum temperature for growth (Braarud, 1961; Hulburt and Guillard, 1968).

VARIATION IN SPECIFIC GROWTH RATE (μ) WITH TEMPERATURE IN LABORATORY CULTURES OF UNICELLULAR ALGAE

Much of the available data on the specific growth rates of algae in culture have been assembled by Hoogenhout and Amesz (1965). Growth rates for marine phytoplankton fall in the same range of values as those for freshwater algae, and there are no obvious distinctions between marine and freshwater unicellular algae with respect to the variation of specific growth rate (μ) with temperature. Hence data for algae from the two media will not be segregated.

Specific growth rate is defined as the rate of increase of cell substance per unit cell substance $1/N\ dN/dt = \mu$. Since dN/dt depends upon the rate of metabolic processes, one expects some temperature variation of μ if conditions are otherwise favorable for growth (i.e., if light and nutrient supply are not growth-rate limiting). This variation can be seen in Figure 1. Data of Figure 1 were selected from Hoogenhout and Amesz (1965) as representing, as nearly as possible, growth rates measured under conditions such that temperature would be rate limiting. Figure 1 shows much variation in μ among species at a given temperature. Most of this results from differences in cell size (Williams, 1964; Eppley and Sloan, 1966; Werner, 1970) and in the concentration of photosynthetic pigments within the cells of the different species (Eppley and Sloan, 1966).

It has been mechanically impossible to identify each of the points on the Figure by species (approximately 130 species or clones were included, some for several temperatures). No doubt, by further literature search, the entire area beneath the line of maximum expected growth rate could be filled in. It is perhaps surprising and a tribute to the quality of the measurements from many laboratories that only three of nearly 200 values were rejected as being unrealistically high. Inclusion of these three spurious values would only be an embarrassment to the authors rather than a critique of the validity of the line of maximum expected growth rate presented.

Not plotted in Figure 1 are values of μ for *Chlamydomonas mundana* photoassimilating acetate (Eppley and Macias R., 1962), *Chlorella pyrenoidosa* 7-11-05 for which μ was computed for increase in cell substance uncoupled from cell division (Sorokin and Krauss, 1962), or for the photosynthetic bacteria listed by Hoogenhout and Amesz (1965). Values for these slightly exceed the line of maximum expected μ. Figure 1 is limited to algae growing photoautotrophically with carbon dioxide and water.

Two general trends are noted in Figure 1: (1) There is a gradual and exponential increase in μ with temperature up to about 40°C. Temperature data above 40°C, obtained with thermophilic, blue-green algae show no further increase in μ (Castenholz, 1969). Such temperatures are outside the range encountered in the ocean and will not be further discussed. (2) Values of μ below 40°C seem to fall within an envelope and it is possible to draw a smooth curve, i.e., a line of maximum expected value, to describe the upper limit of μ to be expected at a given temperature. An approximate equation for this line is:

$$\log_{10} \mu = 0.0275T - 0.070 \qquad (1)$$

where T is temperature in degrees Celsius.

Equation (1) gives a Q_{10} for growth rate of 1.88, slightly lower than expected from the Q_{10} for photosynthesis measured in natural waters (Talling, 1955, gives $Q_{10} = 2.3$; Williams and Murdoch, 1966, give $Q_{10} = 2.25$; Ichimura, 1968, gives $Q_{10} = 2.1$) or the Q_{10} for growth rate of laboratory cultures suggested earlier (Eppley and Sloan, 1966, give $Q_{10} = 2.3$).

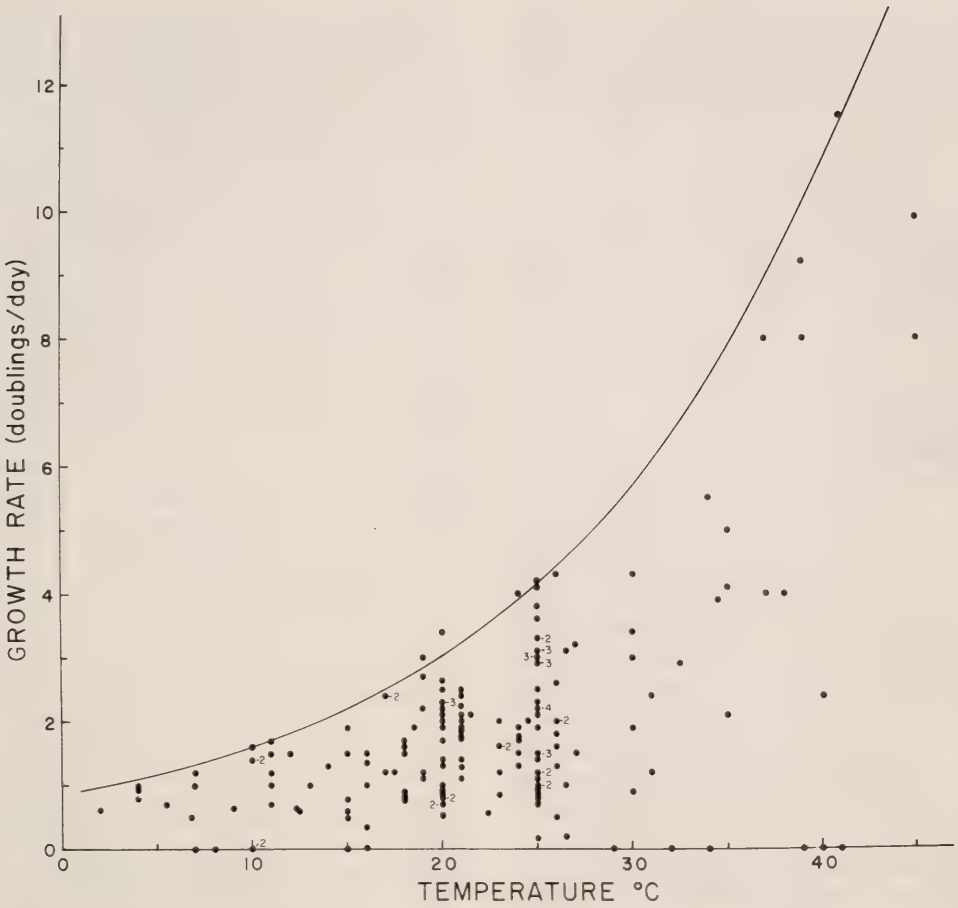

FIGURE 1.—Variation in the specific growth rate (μ) of photoautotrophic unicellular algae with temperature. Data are all for laboratory cultures. Growth rate is expressed in doublings/day. Approximately 80 of the points are from the compilation of Hoogenhout and Amesz (1965). That listing is restricted to maximum growth rates observed, largely in continuous light. The figure also includes additional data, mostly for cultures of marine phytoplankton, from the following sources: Lanskaya (1961), Eppley (1963), Castenholz (1964, 1969), Eppley and Sloan (1966), Swift and Taylor (1966), Thomas (1966), Paasche (1967, 1968), Hulburt and Guillard (1968), Jørgensen (1968), Smayda (1969), Bunt and Lee (1970), Guillard and Myklestad (1970), Ignatiades and Smayda (1970), Polikarpov and Tokareva (1970). The latter papers include about 50 strains of marine phytoplankton. The line is the growth rate predicted by Equation (1), i.e., the line of maximum expected μ. Small numbers by points indicate the number of values which fell on the point.

I will avoid speculation on possible reasons why such a curve would include algae from a wide variety of taxonomic groups, including both eucaryotic and procaryotic cell types, cells with different complements of photosynthetic pigments, and diverse morphologies. Nevertheless, the curve and Equation (1) appear to be useful as a generalization of maximum μ to be expected for photosynthetic unicellular algae.

Equation (1) is essentially a van't Hoff formula and can be expressed in the more typical form

$$\mu = 0.851\ (1.066)^{T}. \qquad (1a)$$

McLaren (1963) discussed the choice of a temperature function and preferred the formula of Bělehrádek

$$\mu = a\ (T - \alpha)^{b} \qquad (1b)$$

where a, b, and α are constants. A virtue of this equation, among the three monotonic functions discussed by McLaren (1963) is that α, the scale positioning factor, represents a "biological zero" for the process. A graph of log (μ) vs. log ($T - \alpha$) assumes linearity for appropriate values of α. Fitting values from Equation (1) at $T = 0$, 10, 20, and 30 degrees gave linear graphs if α were $\leqslant -40$ degrees. For $\alpha = -40$, a and b were approximately 2.46×10^{-6} and 3.45, respectively.

Figure 1 can be made more understandable by comparing μ vs. temperature curves for a few selected species for which fairly complete data are available (Figure 2). Each of these species has a different optimum temperature and the maximum growth rate for each approaches the line of maximum expectation. Such "μ vs. temperature" curves typically show a gradual diminution of μ as temperature decreases from the optimum, but an abrupt decline at supraoptimal temperatures.

Temperature optima and the upper critical temperature can be shifted somewhat by altering environmental conditions. For example, the salinity of the culture medium influences these parameters in euryhaline *Dunaliella tertiolecta* (Figure 3). Note, however, that only one salt concentration gives the unique maximum growth rate of about 5.0 doublings/day.

The figures can be criticized as being limited with respect to the number of species included. Furthermore many of them represent "laboratory weed" species and relatively few are ecologically significant ocean phytoplankton. Happily this shortcoming is temporary and information on important planktonic species is growing (see Figure 1 legend).

Use of Figures 1 and 2 or Equation (1) for insight as to maximum expected values of μ in the sea presumes that natural marine phytoplankton are autotrophic. But it is conceivable,

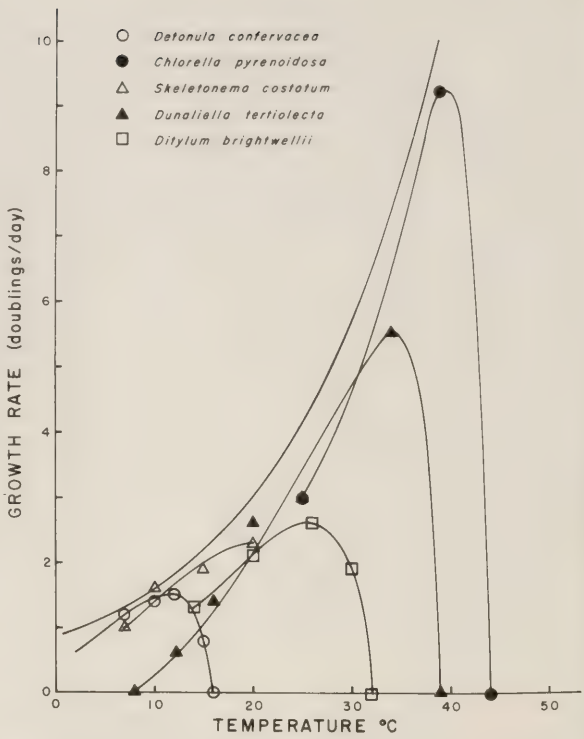

FIGURE 2.—Growth rate vs. temperature curves for five unicellular algae with different temperature optima: *Detonula confervacea* (Guillard and Ryther, 1962; Smayda, 1969), *Skeletonema costatum* (Jørgensen, 1968), *Ditylum brightwellii* (Paasche, 1968), *Dunaliella tertiolecta* (McLachlan, 1960; Ukeles, 1961; Eppley, 1963; Eppley and Sloan, 1966), *Chlorella pyrenoidosa* (Sorokin and Krauss, 1958, 1962).

although perhaps unlikely in the sea, that heterotrophic nutrition might lead to values of μ higher than predicted above, as appears to be the case when one compares doubling times of heterotrophic and photosynthetic bacteria or autotrophic vs. photoheterotrophic growth rates of the sewage alga *Chlamydomonas mundana*.

Equation (1) has been useful in this laboratory for predicting the maximum dilution rates ("washout rates") for continuous cultures. In the few organisms examined here the value of μ at washout was slightly higher than the maximum rate observed in batch cultures of the organism, but within the envelope of values predicted by Equation (1).

Rates of growth given by Equation (1) are much higher than those which permit the operation of mass cultures at maximum efficiency of light utilization or nutrient removal. Maximum production will be achieved when the product of μ and standing stock is a maximum, and light is likely to be limiting growth at some depth in the culture under these conditions (see, for example, Ketchum, Lillick, and Redfield, 1949; Myers and Graham, 1959).

The data of Figures 1 and 2 apply to cultures grown with continuous illumination (or with optimum daylength for those in which μ passes through a maximum at intermediate daylength [Castenholz, 1964; Paasche, 1968]). This lessens the utility of the data for predictive purposes with natural phytoplankton exposed to seasonally varying daylength since the daylength for maximum μ varies among species (Table 1). Efforts to generalize on the influence of daylength on μ have not been very successful since the daylength allowing maximum μ at a given temperature seems to vary with the intensity of illumination (Tamiya et al. 1955; Terborgh and Thimann, 1964). A proportion between μ and the number of hours of light/24 hr is often assumed but this can be only a first approximation.

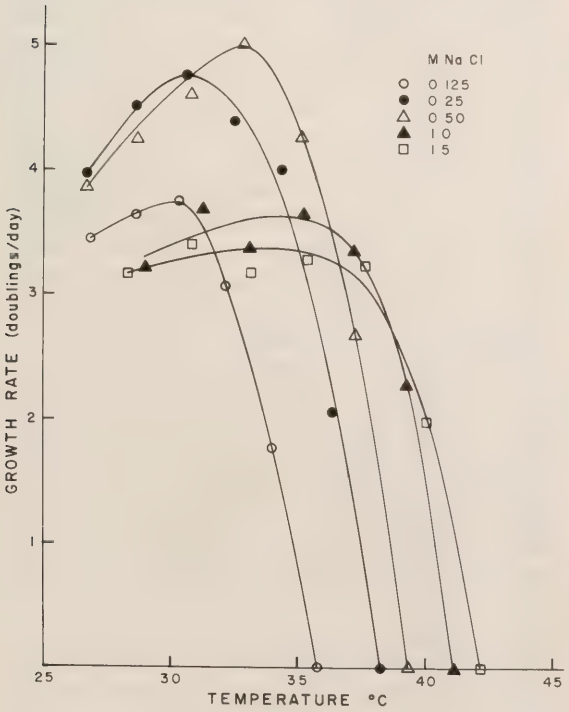

FIGURE 3.—Growth rate vs. temperature curves for *Dunaliella tertiolecta* measured in culture media containing different salt concentrations (R. W. Eppley and F. M. Macias, unpublished data).

TABLE 1.—Daylength resulting in maximum growth rate for some algae which show depressed growth rate in continuous light. Some species which showed maximum μ in 24 hr light/day are shown for comparison.

Organism	Daylength (hr)	Growth rate[1] μ_{max}	Temperature (°C)	Reference
Ditylum brightwellii	16	2.1	20	Paasche (1968)
Nitzschia turgidula	16-24	2.5	20	Paasche (1968)
Fragilaria sp.	24	1.7	11	Castenholz (1964)
Biddulphia sp.	15	1.5	11	Castenholz (1964)
Synedra sp.	15-24	1.2	11	Castenholz (1964)
Melosira sp.	15-24	0.7	11	Castenholz (1964)

[1] Units are doublings/day.

Use of Figure 1 and Equation (1) for insight on the behavior of natural phytoplankton requires the further assumption that the organisms present are reasonably adapted to ambient temperatures and are, preferably, at a temperature somewhat less than optimum. Aruga (1965a) has shown this to be so for the phytoplankton of a pond on the University of Tokyo campus. Smayda (1969) has discussed his own and earlier observations on the distribution of phytoplankton in nature where temperature optima for growth in laboratory cultures were invariably higher by several degrees than the water temperature in which the species flourish.

Figure 2 suggests that μ for suboptimal temperatures will be only slightly lower than would be predicted from the maximum μ for the species given a temperature coefficient (Q_{10}) for growth of about 2. However, some organisms show a critical lower temperature, above the freezing point of water, below which no growth occurs. Ukeles (1961) has listed such lower critical temperatures for several species, and see Smayda (1969) for another example. Temperatures in excess of the optimum for growth result in a much steeper decline in μ with increasing temperature than do suboptimal temperatures; growth in this thermal region would be risky

if the ambient temperature were subject to fluctuations of a few degrees.

ESTIMATES OF THE SPECIFIC GROWTH RATES OF PHYTOPLANKTON IN THE SEA

REVIEW OF METHODS

Measurement of the phytoplankton specific growth rate in nature is not a routine procedure both because of the lack of widely accepted methodology and because the utility of such data is not well appreciated. J.W.G. Lund, J. F. Talling, L. A. Lanskaya, T. J. Smayda, J. D. H. Strickland, and S. Ichimura and his colleagues have been the pioneers in such measurement in natural waters while R. W. Krauss and J. Myers have promoted the measurement of μ for laboratory cultures.

Minimal values of μ can be calculated from rates of increase of cell concentration or of chlorophyll during the spring bloom in temperate waters, although advection, diffusion, and grazing complicate their interpretation. Recent examples of this technique are provided by Bunt and Lee (1970), Pechlaner (1970), and Happey (1970). Samples of water can also be incubated in bottles for cell counting at intervals (see, for example, Talling, 1955; Smayda, 1957). In oligotrophic waters the period of growth necessary to allow a precise estimation is likely to result in the depletion of nutrients and the gradual diminution of μ with time. In rich water if growth were extensive, changes in μ would be expected as a result of the decrease in effective illumination in the bottles due to self-shading. Short-term incubations of less than 24 hr may be complicated by diel periodicity in the property measured, by synchronous cell division, or insufficient change for meaningful calculations. Such problems are eased in shipboard cultures provided with adequate nutrients for growth, but here rates may be unreasonably high if ambient nutrient or light levels in the natural water are not duplicated.

Estimates of μ are obtained routinely in terms of ^{15}N-nitrogen assimilation rate per unit particulate nitrogen in the sample, but such rates will underestimate μ to the extent that the particulate nitrogen analyzed includes detrital and other nonphytoplankton nitrogen (Dugdale and Goering, 1967).

Carbon assimilation rates per unit phytoplankton carbon have also been calculated but suffer from the errors inherent in measuring the latter as well as from the uncertain reality of incubation conditions (Riley, Stommel, and Bumpus, 1949; McAllister, Parsons, and Strickland, 1960; McAllister et al., 1961; Antia et al., 1963; McAllister, Shah, and Strickland, 1964; Strickland, Holm-Hansen, Eppley, and Linn, 1969). What is needed is an instantaneous method not confounded by the complexities of long incubation either in situ, in enclosed vessels, or in shipboard cultures. Unfortunately, no such method is in view.

In this laboratory two methods have been employed for estimating the carbon content of the crop. In the first of these, all the cells in the sample are counted and their dimensions measured so that the cell volume of each species can be calculated (see Kovala and Larrance, 1966, for dealing with cell shape problems). The carbon content of a cell is then computed from its volume, or "plasma volume," using empirical equations developed from laboratory culture (Mullin, Sloan, and Eppley, 1966; Strathmann, 1967). The carbon in each species is then obtained from the concentration of cells of that species, and the total carbon of all species is summed. Several applications of this method have been published (Strickland, Eppley, and Rojas de Mendiola, 1969; Holm-Hansen, 1969; Eppley, Reid, and Strickland, 1970; Reid, Fuglister, and Jordan, 1970; Zeitzschel, 1970; Beers et al., 1971; Hobson, 1971; Eppley et al., in press). In the second method, only recently put into practice, the adenosine triphosphate (ATP) content of particulate matter retained on a fine porosity filter is determined (Holm-Hansen and Booth, 1966). The ATP is apparently restricted to living cells but may include contributions from bacteria, protozoans, and other colorless microorganisms, as well as phytoplankton, even if larger animals are removed by passing the sample through netting. However, phytoplankton appear to be predominant in water samples from

the euphotic zone judged from the rough proportionality of ATP to chlorophyll. Estimates derived from ATP appear to agree well with those given by the first method (Holm-Hansen, 1969) and the ratio C/ATP approximates 250.

In determining an average μ for the phytoplankton the carbon content, as measured above, is taken at the beginning of the photosynthesis measurement to give phytoplankton carbon at time zero (C_0). The measured daily rate of photosynthetic carbon assimilation, assumed to represent net carbon assimilation (ΔC), is then added to the carbon content after a day's growth. The specific growth rate is then calculated as:

$$\mu = \frac{1}{t} \log_2 \left(\frac{C_0 + \Delta C}{C_0}\right) \qquad (2)$$

to give μ in doublings of cell carbon per day.

It should be straightforward to compute μ using ATP determined initially and after 24-hr incubation, and this has been done at least once (Sutcliffe, Sheldon, and Prakash, 1970). We have used chlorophyll *a* values, before and after 24- or 48-hr incubation, to compute μ but the results were poor due to the plasticity of cell chlorophyll *a* content and the difficulty of providing incubation conditions sufficiently close to those in nature to maintain constant cell chlorophyll *a* per cell or per weight of carbon (Eppley, 1968).

Increase in the total volume of particulate matter, determined with an electronic particle counting and sizing machine, can also be used to compute μ (Parsons, 1965; Cushing and Nicholson, 1966; Sheldon and Parsons, 1967). This method holds much promise when changes are large enough to be significant over background levels of particulates. The cost of the machines is a serious drawback to wider use, and the problems in proper incubation of the sample to mimic conditions in the sea are as serious here as in the other incubation methods.

Sweeney and Hastings (1958) used the percentage of paired dinoflagellate cells in cultures as a measure of the time of day of cell division and this has been used at sea (R. Doyle, Duke University, personal communication). A variation on this theme has allowed estimates of μ for *Pyrocystis* species in situ (E. Swift, University of Rhode Island, personal communication). Changes in cell morphology related to cell division probably give the least ambiguous estimates of μ where advection and sinking are not serious problems and when a parcel of water can be followed over time. The time course of change in valve diameter in diatoms seems to be out of favor for estimating μ since valve diameter in cultures may not decrease in a regular way or always be proportional to the number of cell divisions. Methods of measuring microbial growth rates were recently reviewed by Brock (1971).

RESULTS OF GROWTH RATE MEASUREMENTS IN THE NATURAL PHYTOPLANKTON AT DIFFERENT TEMPERATURES

In their classic paper of 1949, Riley, Stommel, and Bumpus expressed photosynthetic rate as the daily carbon assimilation per unit plant carbon, a measure readily calculated as μ in doublings/day. They used Baly's equation as a model. This equation includes temperature as a variable influencing photosynthetic rate. The constants in the equation were computed from Baly's compilation of data on *Chlorella* cultures and detached leaves, and from Jenkin's 1937 data for a culture of *Coscinodiscus* incubated at various depths in the sea. I have calculated expected values of μ using their Equation 6 for different levels of total incident radiation (Figure 4). It is seen that the Baly equation is relatively insensitive to temperature, in comparison to Figure 1, and gives values inconsistent with the results from laboratory cultures.

Bunt and Lee (1970) provide a unique set of data on the photosynthetic rates of Antarctic phytoplankton which grow under the ice layer, an environment with low ambient light and with temperature approximately —2°C. They also provide seasonal values of the particulate carbon and chlorophyll *a* concentration. A maximum, midsummer, value of μ was less than 0.5 doublings of cell carbon/day.

Most of the data which allow estimates of μ are from nutrient-poor waters, such as are found

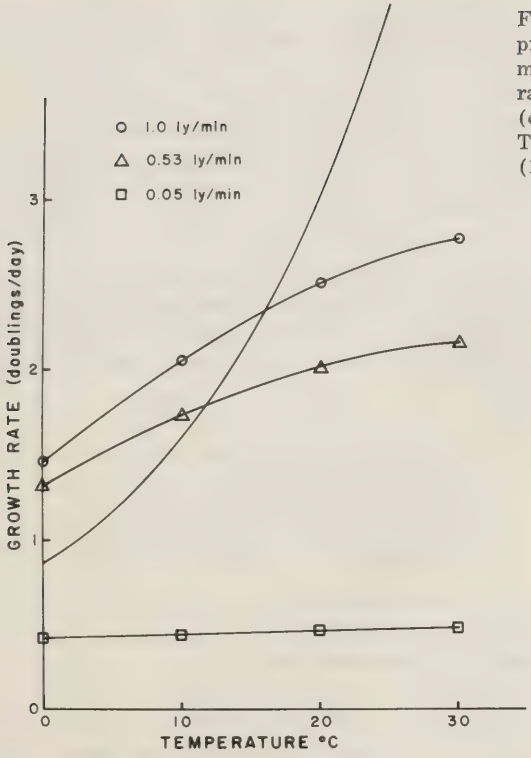

FIGURE 4.—Growth rate vs. temperature relationship predicted by the Baly equation as used by Riley, Stommel, and Bumpus (1949). Three different levels of total radiant energy are included for the Baly equation: 1.0 (circles), 0.53 (triangles), and 0.05 ly/min (squares). The line of maximum expectation predicted by Equation (1) is drawn for comparison (no symbols).

in the Sargasso Sea, the Eastern Tropical Pacific, and southern California coastal waters. Exceptions are μ estimates obtained from upwelling regions off Peru (Strickland, Eppley, and Rojas de Mendiola, 1969; Beers et al., 1971) and southwest Africa (Hobson, 1971) where nutrient limitation is not a factor reducing μ.

A summary of estimated values of μ, as average doublings of cell carbon/day in the euphotic zone, is provided in Table 2. The recent data are based upon simulated in situ techniques usually involving 24-hr incubation in order to obtain photosynthetic rates free of errors resulting from diel periodicity in metabolism. The list of values given is not inclusive but is, hopefully, representative. Mean values of μ in the Peru Current showed little variation and averaged about 0.7 doubling/day. Values of this magnitude are consistent also with estimates from ^{15}N-labeled nitrate assimilation rates measured by R. C. Dugdale, J. J. Goering, and

TABLE 2.—Some estimates of the average specific growth rate of phytoplankton in the euphotic zone for various regions. Temperatures indicated are for the surface or the average in the mixed layer.

Location	Temperature (°C)	Growth rate as doublings/day		Reference
		Measured	Max. expected	
		Oligotrophic waters		
Sargasso Sea	--	0.26	--	Riley, Stommel, and Bumpus (1949)
Florida Strait	--	0.45	--	Riley, Stommel, and Bumpus (1949)
Off the Carolinas	--	0.37	--	Riley, Stommel, and Bumpus (1949)
Off Montauk Pt.	--	0.35	--	Riley, Stommel, and Bumpus (1949)
Off southern California				
July 1970	20	0.25-0.4	1.5	Eppley et al. (in press)
Apr.-Sept. 1967	12-21	0.7 avg	0.9-1.6	Eppley et al. (1970)
		Nutrient-rich waters		
Peru Current				
Apr. 1966	17-20	0.67 avg	1.5	Strickland, Eppley, and Rojas de Mendiola (1969)
June 1969	18-19	0.73 avg	1.4	Beers et al. (1971)
Off S.W. Africa	--	1.0 avg	--	Calculated from Hobson (1971)
Western Arabian Sea	27-28	>1.0 avg	2.4	Calculated from Ryther and Menzel (1965b)

[1] From Equation (1) assuming μ will be one-half the value calculated as expected if daylength is 12 hr and μ is directly proportional to the number of hours of light per day.

co-workers (University of Washington, 1970) in the Peru upwelling region.

The maximum values of μ observed in depth profiles off Peru approached those expected from Figure 1 if the effect of daylength is considered (Figure 5) but were lower as a result of low insolation brought about by continuous cloud cover. Depth profiles of μ roughly parallel those for photosynthetic rate per weight of chlorophyll *a* and both show diminished rates with depth as a result of decreasing light.

Figure 5 also shows a depth profile of μ for the North Central Pacific where μ was depressed because of low ambient nutrient concentrations. Enrichment experiments suggested that growth rate was limited at two stations by low concentrations of both nitrogen and phosphorus and at a third station by nitrogen alone (Perry, in press).

Thomas (1970b) and Thomas and Owen (1971) reported values of μ for 10 m depths in the eastern tropical Pacific Ocean. In situ μ was estimated to be about 0.2 doubling/day resulting from low ambient nitrogen concentration. Shipboard cultures were enriched with various concentrations of nitrogen (nitrate and ammonium), and the variation of μ with nitrogen concentration was determined (Thomas, 1970b). Maximum values of μ were 1.1-1.5 doublings/day.

In many cases nutrient limitation (in the upper surface waters) or light limitation (in deeper waters and in nonstratified water where vertical mixing may reduce the effective light level to which the phytoplankton are exposed) appears to decrease μ. The values expected from Figure 1 are not realized under such conditions and μ shows little or no temperature-dependence.

Table 3 presents growth rates measured by three different methods (i.e., from the velocity of nitrogen assimilation per unit particulate nitrogen, from the photosynthetic carbon assimilation rate per unit phytoplankton carbon, where the carbon content of the phytoplankton crop was determined from ATP, and from cell concentration and cell volume). Growth rates from the three methods usually agree within a factor of two, but more precise methods are desirable. The value from ^{15}N assimilation rate

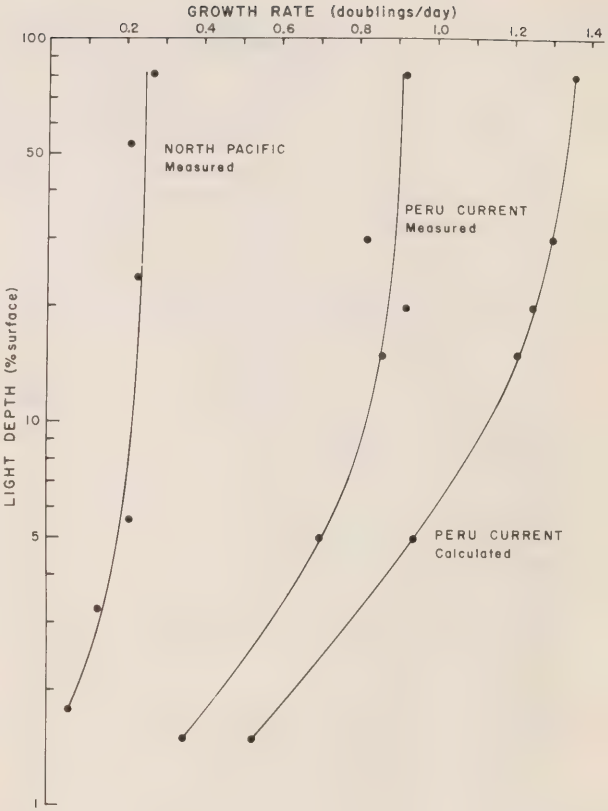

FIGURE 5.—Variation in growth rate of natural marine phytoplankton with depth in the Peru Current, June 1969, and in the subtropical North Pacific central gyre, November 1971 (this laboratory, unpublished). The "light depth" of the ordinate was calculated as the radiant energy at depth as a percentage of that at the surface so that data from the two regions, with euphotic zone depths of about 30 and about 150 m, could be compared. The calculated line is based on Equation (1) for 19°C with the assumption that light limits growth rate below the surface. The μ_{max} from Equation (1) was multiplied by $(I/2.5 + I)$ where I is the radiant energy at depth as percent of surface. The half-saturation constant of 2.5% is low (see Rodhe, 1965) and suggests that the Peru Current phytoplankton were "shade adapted." Hence, measured μ would be less than expected from Equation (1), in spite of abundant nutrients. In the North Pacific study enrichment experiments and other data suggested limitation of phytoplankton growth rate by both nitrogen and phosphorus concentration (Perry, Renger, Eppley, and Venrick, unpublished data). There the temperature in the mixed layer was 22°C and the maximum expected value would be slightly greater than shown for the Peru Current.

TABLE 3.—Some comparison of the average growth rate of phytoplankton in the euphotic zone in southern California coastal waters using different methods of estimation.

Month	Station	Photosynthetic rate (g C/m²/day)	Standing stock (g C/m²) From ATP	Standing stock (g C/m²) From cell vol.	Growth rate (doubling/day) by method (a)	(b)	(c)
June 1970	4	0.53	2.4	2.0	0.28	0.33	0.13
	7	1.05	3.1	3.25	0.42	0.40	--
July 1970	1	1.37	8.4	--	0.26	--	0.19
	6	1.10	4.4	--	0.32	--	0.22
	10	0.36	3.6	--	0.13	--	0.21
	19	1.76	5.9	5.38	0.37	0.40	0.15

[1] Methods: (a) μ from photosynthetic rate and ATP × 250 = standing stock as carbon.
(b) μ from photosynthetic rate and standing stock carbon computed from cell numbers and cell volumes.
(c) μ computed from assimilation rate of nitrate + ammonium + urea per unit particulate nitrogen. Data for method (c) from McCarthy (1971) and Institute of Marine Resources (1972, see text footnote 2). Other data are unpublished values from this laboratory. Surface water temperatures were 18°-20°C. Maximum expected growth rates would be about 1.5 doublings/day.

tends to be lower than those from ^{14}C assimilation rate because no correction was made for the detrital nitrogen in the particulate matter, while detrital carbon is not a complication in the other methods. Low growth rates in these samples resulted from nitrogen limitation.

Rates of nitrogen assimilation per weight of particulate N were measured in the Sargasso Sea and Peru upwelling regions (Dugdale and Goering, 1967; Dugdale and MacIsaac, 1971), and in the eastern tropical Pacific Ocean (Goering, Wallen, and Nauman, 1970) which allow estimates of μ.

As is readily seen from the above discussion and the values of Tables 2 and 3 we have very little data at hand to properly evaluate the role of temperature in determining maximum rates of phytoplankton growth in the sea, and whether Figures 1 and 2 and Equation (1) are useful guides for field work. It is hoped that this lack will stimulate more effort to make growth rate measurements. Most needed are μ values for cold waters and warm, nutrient-rich waters.

Meantime let us turn to lakes and ponds. Additional growth rate data are available and the influence of temperature on growth rate is often apparent. Since growth rates seem comparable in laboratory cultures for freshwater and marine unicellular algae, as noted earlier, μ vs. temperature in lakes should be of equal interest to limnology and oceanography. Some data are given in Table 4 which confirm low μ values in cold water and a variation in μ with temperature in outdoor ponds.

The phytoplankton growth rates in lakes which show a variation in μ with temperature were usually measured in the spring as the waters were gradually warming but before nutrients were depleted to levels limiting to the rate of phytoplankton growth (cf. Cannon, Lund, and Sieminska, 1961). Presumably similar data could be gathered for nutrient-rich estuaries or for temperate, coastal sea areas where sufficient warming occurs to obtain a reasonable range of temperatures before stratification and nutrient depletion become severe. The seasonal succession of phytoplankton in coastal ocean waters has been much studied, and the change in the phytoplankton crop from predominantly diatoms to flagellates, with the onset of nutrient depletion, would be accompanied by a marked decrease in growth rate. One may judge the magnitude of change from the comparison of μ in the Peru Current with μ in the North Pacific central gyre (Figure 5).

INTERRELATION BETWEEN SPECIFIC GROWTH RATE OF PHYTOPLANKTON AND ASSIMILATION NUMBER

The specific growth rate of phytoplankton in laboratory cultures is often measured from the rate of increase in the concentration of cells in the culture when cell counts are determined over a time interval, i.e.,

$$\mu = \frac{1}{\Delta t} \log_2 \left(\frac{N_2}{N_1}\right). \qquad (3)$$

This can also be expressed as

$$\mu = \frac{1}{\Delta t} \log_2 \left(\frac{N_1 + \Delta N}{N_1}\right) \qquad (4)$$

where N_1 is the initial cell concentration, N_2 the cell concentration after an interval of time, Δt, and ΔN is $N_2 - N_1$. To determine μ from analogous carbon units one needs the initial carbon content of the phytoplankton (C_1) and either the carbon content after a time interval Δt, i.e., C_2, or a measure of carbon assimilation by the phytoplankton during the time interval, i.e., ΔC. It will be assumed that the ^{14}C method of measuring phytoplankton photosynthesis (Steemann Nielsen, 1952) in fact measures ΔC, the net increase in particulate carbon in the phytoplankton. This is indicated by several studies with laboratory cultures which include two or more independent measures of the rate of carbon assimilation by the phytoplankton cells (Antia et al., 1963; McAllister et al., 1964; Eppley and Sloan, 1965; Ryther and Menzel, 1965a; Strickland, Holm-Hansen, Eppley, and Linn, 1969). Then μ can be calculated from carbon data from Equation (2). The evaluation of μ requires a measurement of photosynthetic rate as carbon and an estimate of the carbon content of the phytoplankton at the initiation of the measurement. Direct methods for the latter are not usually suitable because of detrital carbon in natural waters and indirect methods must often serve (see earlier discussion of methods of measuring μ). A convenient way of expressing photosynthetic rate per unit phytoplankton standing stock is the "assimilation number," i.e., the rate of photosynthetic carbon assimilation per weight of chlorophyll *a*. The terms "assimilation ratio" and "photosynthetic index" are common synonyms for assimilation number. If the carbon/chlorophyll *a* ratio in the phytoplankton is known, its carbon content can, of course, be calculated from chlorophyll measurements. Usually this is not the case and considerable effort has been expended to derive such estimates (see, for example, Harris and Riley, 1956; Cushing, 1958; Wright, 1959; Steele and Baird, 1961, 1962; Lorenzen, 1968; Eppley, 1968; Zeitzschel, 1970; Hobson, 1971). An equation expressing μ (as doublings of cell carbon/day) in terms of the assimilation number per day and the carbon/chlorophyll ration of the phytoplankton can be derived from Equation (2) as

$$\mu = \frac{1}{\Delta t} \log_2 \left(\frac{\text{C/Chl. } a + \Delta\text{C/Chl. } a}{\text{C/Chl. } a}\right). \qquad (5)$$

This equation is useful in that it directly relates the assimilation number, i.e., the photosynthetic rate per weight of chlorophyll (ΔC/Chl. *a*), the carbon/chlorophyll *a* ratio of the phytoplankton

TABLE 4.—Phytoplankton growth rates in lakes and ponds.

Organism	Temperature (°C)	Growth rate as doublings/day		Reference
		Measured	Max. expected[1]	
		1-m depth only		
Asterionella formosa	5	0.8	1.2	Talling (1955)
		Average in the lake		
Stephanodiscus hantzschii	2-4	0.3	1.1	Pechlaner (1970)
Asterionella formosa	5	0.3	1.2	Happey (1970)
Stephanodiscus rotula	8	0.25	1.4	Happey (1970)
	15	0.7	2.2	Happey (1970)
		In outdoor ponds		
Chlorella ellipsoidea	7	0.15	1.3	Tamiya et al. (1955)
	15	0.65	2.2	
	25	1.4	4.1	

[1] From Equation (1).

(C/Chl. *a*), and μ. Figures 6 and 7 show this relationship graphically where the calculated assimilation number per day (Figure 6) or per hour (Figure 7) is graphed as a function of μ for different carbon/chlorophyll *a* ratios in the crop. Carbon/chlorophyll ratios of Figures 6 and 7 are typical of the Peru upwelling region (C/Chl. *a* 30-40) (Lorenzen, 1968; Strickland, Eppley, and Rojas de Mendiola, 1969; Beers et al., 1971) and the Western Arabian Sea (Ryther and Menzel, 1965b), or low-nutrient surface waters off southern California (90-100) (Eppley, 1968; Strickland, 1970); and of surface waters in the North Pacific central gyre (120-150) (Institute of Marine Resources, unpublished data). The marked dependence of the assimilation number upon the carbon/chlorophyll *a* ratio of the phytoplankton is noteworthy, although little discussed in the literature. It is interesting that assimilation numbers greater than about 15 per hour (see Figure 7) are rarely reported in the literature and one wonders whether this is because of disbelief in the validity of the data or because high μ and high C/Chl. *a* are somehow mutually exclusive in nature. The latter is most likely since such high assimilation rates and high μ would place extreme demands for nutrients, such as N and P, on the environment and could not long be sustained without massive nutrient input. Even at southern California sewage outfalls where high rates of nutrient input prevail we found low values for μ. These low values apparently result from the buildup of high phytoplankton crops which maintain low-nutrient levels in the surface waters such that growth rate is nitrogen-limited (Institute of Marine Resources).[2] Furthermore, high C/Chl. *a* ratios seem to be typical of nutrient depleted cells which grow slowly. For example, carbon/chlorophyll *a* ratios increased from 30 to over 150 with increasing nitrogen limitation of growth in N-limited chemostat cultures of marine phytoplankton (Thomas and Dodson, in press; Institute of Marine Resources[2]).

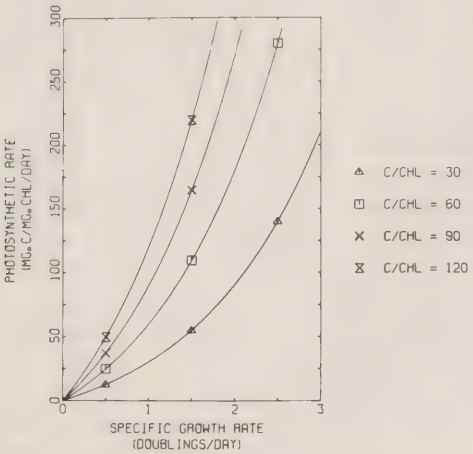

FIGURE 6.—Photosynthetic rate (assimilation number/day) vs. the specific growth rate of the phytoplankton computed from Equation (5). Photosynthetic rate is expressed as milligrams carbon assimilated per day per milligram chlorophyll *a* and is shown for several values of the ratio carbon/chlorophyll *a* in the phytoplankton crop (30, 60, 90, and 120 g/g).

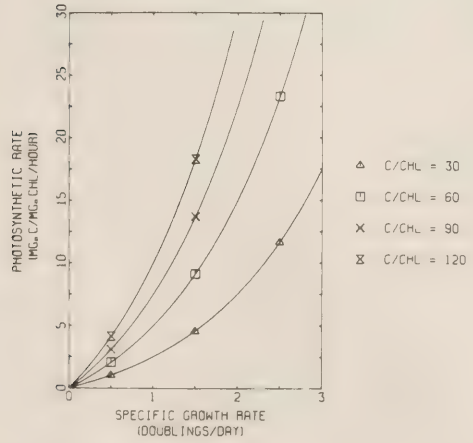

FIGURE 7.—Same as Figure 6, but photosynthetic rates (assimilation numbers) were calculated per hour, rather than per day, assuming 12 hr light per day (i.e., values of Figure 6 were divided by 12).

[2] Institute of Marine Resources. 1972. Eutrophication in coastal waters: nitrogen as a controlling factor. Final Rep. U.S. Environ. Prot. Agency, Proj. #16010 EHC. Inst. Mar. Resour., Univ. Calif., San Diego. 67 p.

THE VARIATION OF ASSIMILATION NUMBER WITH TEMPERATURE IN THE SEA

The maximum expected values of μ at different temperatures, from Equation (1), can be used to predict maximum assimilation numbers to be expected in the sea (as grams carbon/gram chlorophyll *a* per time). Combining Equations (1) and (5) gives rise to Figures 8 and 9 to show assimilation numbers per day and per hour for different C/Chl. *a* ratios in the phytoplankton. Actual rates would be lower than those shown for the reasons already discussed and would require the growth of small-celled phytoplankters with light essentially saturating for photosynthesis and with adequate nutrient concentrations. Aruga (1965b) presents graphs of assimilation numbers vs. temperature, with various light levels, for *Scenedesmus* sp. grown at 20°C. His curves resemble these in form.

The question of the influence of daylength upon μ is ignored in Figure 8 and needs further investigation before generalities may be drawn. In Figure 9 it was assumed that μ in natural phytoplankton assemblages will be one-half the value calculated from Equation (1) since that function assumes continuous light rather than natural illumination of, on the average, 12 hr light and 12 hr dark.

There are several reasons why the dramatic potential effects of temperature on assimilation number are not often observed in oceanic studies and why so little variation in assimilation numbers has been observed (cf. Ryther and Yentsch, 1958; Curl and Small, 1965). One of these is that growth at different temperatures results in shifts in the chemical composition of phytoplankton. Increased C/Chl. *a* ratios at low temperature would tend to increase assimilation numbers in cold waters over those predicted by Figures 8 and 9 and a constant C/Chl. *a* ratio cannot be assumed.

Steemann Nielsen and Jørgensen (1968a, b) point out that while the lowering of the temperature of a culture of *Skeletonema costatum* reduced the growth rate (by an amount to be expected from Figure 1 and Equation (1)), the

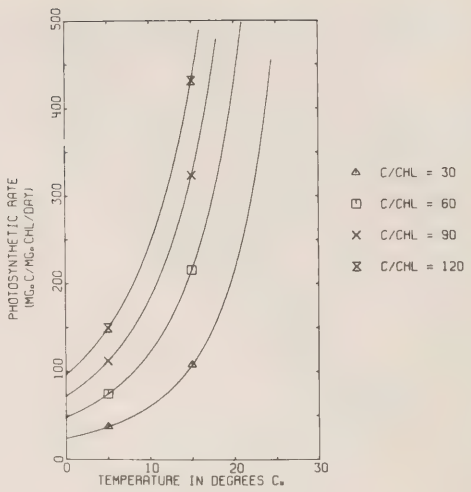

FIGURE 8.—The variation in maximum expected rate of photosynthesis (assimilation number) with temperature. Rates were computed by combining Equations (1) and (5) and are expressed as milligrams carbon/milligram chlorophyll *a*/day. Continuous light was assumed.

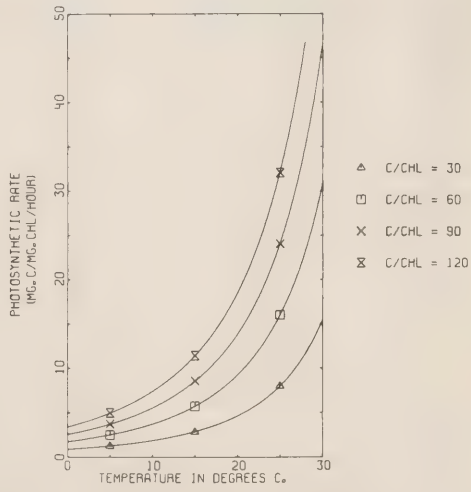

FIGURE 9.—Maximum expected photosynthetic rate (assimilation number) from Equations (1) and (5) with the assumption that the growth rate will be one-half the value predicted by Equation (1) to adjust for natural daylength averaging 12 hr light/day. Photosynthetic rates are expressed as milligrams carbon assimilated/milligram chlorophylll *a*/hour. This figure gives values more in line with ocean measurements than does Figure 8.

photosynthetic rate at light saturation was decreased by a lesser amount. Assimilation numbers for *S. costatum* at 2° or 8°C were higher than would be expected from Figure 9, if it were assumed that a constant C/Chl. *a* ratio was maintained at all temperatures. They observed that cells at low temperature contained greater amounts of photosynthetic enzymes and of organic matter than at higher temperatures. For example, *S. costatum* assimilated 10.2 picogram (pg) carbon/cell in one generation at 20°C, but 19.5 pg at 7°C (Jørgensen, 1968). The carbon content of a cell nearly doubled between 20° and 7°C. *Dunaliella tertiolecta* cells were likewise larger at low temperature than at high temperatures as were cells of *Ditylum brightwellii* (Table 5). This phenomenon seems to be general for mesothermal marine phytoplankton, but data for cold water species are not available. Fluctuations in C/cell and in the C/Chl. *a* are about twofold over the 10°-15°C range studied (Table 5). Steele and Baird (1962) reported high C/Chl. *a* ratios in winter in Loch Nevis and suggested that they resulted from low light "etiolation." One wonders if low winter temperatures might also play a role in this.

We have seen that low temperature reduces the assimilation number and promotes increased carbon/chlorophyll *a* ratios. Similar effects result from nutrient deficiency and were well documented by McAllister, et al. (1964). An influence of nutrient deficiency on μ was shown also in Figure 5 for the North Pacific and was noted in the eastern tropical Pacific (Thomas, 1970b). Low assimilation numbers for phytoplankton photosynthesis in nutrient-impoverished waters are well known (Curl and Small, 1965) and are clearly shown by Ichimura (1967; see his graph of assimilation number vs. phosphate concentration in the waters of Tokyo Bay). Caperon, Cattell, and Krasnick (1971) reported 10 year increases in assimilation numbers in Kaneohe Bay, Oahu, Hawaii (from approximately 6-8 to 11-13 between 1960 and 1970) which attended increased rates of waste discharge into the bay. Hepher (1962) found assimilation numbers of about 4 in unfertilized fish ponds while values in fertilized ponds averaged about 7.6. Furthermore, there are many examples of enhanced ^{14}C-assimilation rates in shipboard enrichment experiments in response to nutrient additions. A recent report is that

TABLE 5.—Carbon content of a cell and carbon/chlorophyll *a* ratios in phytoplankton cultured at different temperatures.

Organism	Carbon/cell	C/Chl./*a*	Temperature	Reference
Skeletonema costatum	19.5	--	7	Jørgensen (1968)
	16.5	--	10	Jørgensen (1968)
	12.7	--	15	Jørgensen (1968)
	10.2	--	20	Jørgensen (1968)
Ditylum brightwellii[1]	1600	41	5	Checkley (1972)[2]
	1500	48	7.5	Checkley (1972)[2]
	1330	50	10	Checkley (1972)[2]
	720	25	15	Checkley (1972)[2]
	--	20	14.5	Strickland, Holm-Hansen, Eppley, and Linn (1969)
	680	14	20	Eppley, Holmes, and Paasche (1967)
Dunaliella tertiolecta[3]	41.8	38	12	Eppley and Sloan (1966)
	35.6	29	16	Eppley and Sloan (1966)
	25.9	25	19.5	Eppley and Sloan (1966)
	28.2	24	20	Eppley and Sloan (1966)
	25.3	26	21	Eppley and Sloan (1966)
	22.5	16	25	Eppley and Sloan (1966)

[1] *D. brightwellii* was cultured with irradiance 0.05 cal/cm²/min with periodic illumination 12L : 12D by Checkley (1972, see footnote 2 below). Values are for samples at the beginning of the light period.

[2] Checkley, D. 1972. The effect of the variation of growth temperature on the ratio of carbon to chlorophyll *a* in a laboratory culture of *Ditylum brightwellii*. Univ. Calif., Inst. Mar. Resour., La Jolla, Calif. (Unpubl. manuscr.)

[3] *D. tertiolecta* was cultured under continuous light with irradiance 0.07 cal/cm²/min.

of Glooschenko and Curl (1971). These authors, and Thomas (1969, 1970a), found no enhancement in waters in upwelling regions, but assimilation numbers were increased in response to nutrient additions in oligotrophic subtropical water. Malone (1971a, b, c) found assimilation numbers in eutrophic waters to be nearly an order of magnitude greater than those in oligotrophic surface waters of the subtropical and tropical Pacific.

It has so far proved difficult to sort out the effects on assimilation number of low light and low temperature in seasonal studies of natural waters. Phytoplankton cultures grown with either low light or low temperature show low maximum photosynthetic rates per chlorophyll *a* at light saturation (P_{max}) and low saturating intensity (I_k) for photosynthesis (Talling, 1957; Steemann Nielsen and Hansen, 1959, 1961; Ichimura, 1960; Yentsch and Lee, 1966). Thus some of the effects on assimilation number usually attributed to low light levels may, in cold waters, result also from low temperature. Bunt and Lee (1970) were able to sort out the two variables in their study of diatom growth under the ice in Antarctica by comparing a station with clear ice to one with snow cover. Photosynthetic rate and growth rate were considered to be light-limited at the station with snow cover but temperature-limited at the clear ice station (see also Saijo and Sakamoto, 1964, for photosynthesis vs. depth curves in ice-free and ice-covered lakes).

Assimilation numbers in Antarctic waters are low. Many values are less than 1.0 per hour (Mandelli and Burkholder, 1966; Horne, Fogg, and Eagle, 1969; Bunt and Lee, 1970). Saijo and Kawashima (1964) found an average value of 1.2 mg C/mg Chl. *a*/hr which they attributed to low temperatures and to a deep mixed layer (resulting in a low average irradiance seen by a cell). Water temperature in these studies was usually in the range —2° to 1°C. El-Sayed and Mandelli (1965) gave a range of 1.0 to 3.6 for the assimilation number in surface samples over a temperature range —1.75° to 6.0°C. Assimilation numbers of 4-5 were found in Drake Passage and Bransfield Strait where water temperature was usually about 1°C (El-Sayed, Mandelli, and Sugimura, 1964). All these values are compatible with assimilation numbers predicted by Figure 9.

Besides shifts in carbon/chlorophyll *a* ratios with temperature and the effects of nutrient limitation and light on assimilation number there is yet another factor which tends to obscure the expected seasonal changes in assimilation number with temperature. This comes about as a result of the variation in growth rate and assimilation number with cell size. By passing a water sample through netting one can conveniently separate the phytoplankton into two size categories: the larger cells and diatom chains retained by the net (the netplankton) and the smaller cells and chains which pass through the net (the nanoplankton). Malone (1971a, b, c) has recently compared assimilation numbers of the two size fractions and cites earlier studies. Invariably, the nanoplankton showed higher assimilation numbers than the netplankton, as would be expected from laboratory studies (cited earlier) which show a regular diminution in growth rate with increasing cell size. He further showed that netplankton are relatively more abundant during upwelling in coastal waters off California (Malone, 1971b). Chain-forming diatoms seem to be characteristic of the rich waters of temperate regions during the spring bloom. Yentsch and Ryther (1959) have shown a progressive increase in the ratio nanoplankton/netplankton with seasonally increasing temperature off New England. Tropical, warm, oligotrophic waters have been shown repeatedly to contain a high proportion of nanoplankton (see references cited by Malone and by Sutcliffe et al., 1970).

The causes of such seasonal succession of phytoplankton species is one of the significant problems in the study of marine phytoplankton. One can only speculate on possible contributing factors. For example, the high (relative) sinking rates of large-celled species and long diatom chains suggest that suspension and buoyancy are more significant problems for large cells than small (Munk and Riley, 1952; Smayda, 1970). Hence stratification, reduced mixing, and the imposition of a seasonal thermocline would tend to discourage large forms. Perhaps the most ele-

gant work in such problems is that of Lund and colleagues on diatom succession in the English lakes. Artificially mixing a lake in summer, when it would normally be stratified, permitted a bloom of *Melosira italica*, a diatom which usually sinks out of the water column upon the formation of a thermocline in late spring (Lund, 1971).

Another factor which tends to select against large-celled species in low-nutrient waters results from a low surface/volume ratio and a consequent inability to absorb nutrients from low concentration (Munk and Riley, 1952). This generalization has been confirmed in laboratory experiments on the kinetics of nutrient absorption where large-celled species showed higher half-saturation constants (K_s) for nitrate and ammonium uptake than small-celled species (Eppley, Rogers, and McCarthy, 1969). Similarly, the K_s for assimilation of vitamin B_{12} by phytoplankton depends on cell size (Carlucci, 1972).[3]

The argument with respect to netplankton vs. nanoplankton and the expected seasonal changes in assimilation number with temperature can be summarized as follows: (1) Nanoplankton show higher assimilation numbers (and growth rates) than do netplankton. This generalization results both from observations of natural phytoplankton and from studies of variations with cell size in laboratory cultures. (2) Increasing insolation in the spring results in increased water temperatures, and often in stratification and seasonal thermoclines. Nutrients in the mixed layer then tend to be depleted and often rather quickly, except in very shallow water where regenerative activities of microorganisms in sediments can maintain adequate nutrient levels for rapid phytoplankton growth. (3) Stratification of the water column tends to discourage the growth of large-celled species and long chain diatoms, because (a) reduced vertical mixing may result in their sinking out of the water column and (b) they are less effective in absorbing nutrients from low ambient concentrations than are nanoplankton. (4) Both seasonal increase in temperature and in the ratio of nanoplankton/netplankton should increase assimilation numbers for photosynthesis except where growth and photosynthetic rates are reduced by nutrient limitation.

Nanoplankton would be expected to be more abundant, relative to netplankton, in oligotrophic waters because of their lower sinking rates and lower K_s values for nutrient absorption. Hence, phytoplankton of warm, oligotrophic tropical waters would be expected to show high assimilation numbers (and growth rates) except for effects of nutrient limitation. One can begin to understand from all this why a graph of assimilation number vs. temperature for observation of natural phytoplankton usually fails to show the relationship expected from Figure 9, and why so much current work emphasizes the role of nutrient concentrations in phytoplankton growth in the sea.

Some exceptional marine waters which do show the expected relationship between assimilation number and temperature are shallow coastal estuaries where nutrient regeneration on the bottom maintains a high nutrient input to the overlying water. Examples reported for the east coast of the United States are Barlow, Lorenzen, and Myren (1963), Williams and Murdoch (1966), and Mandelli et al. (1970). Both of the latter papers show graphs of assimilation number vs. temperature which match beautifully the relation expected in Figure 9. Williams and Murdoch's data fall between the C/Chl. *a* 30 and 60 lines, with an indication of higher C/Chl. *a* ratio in winter, as expected. Mandelli et al. present two graphs, one for diatoms and the other for dinoflagellates. Assimilation numbers of the latter are higher than those for diatoms and fall on the line in Figure 9 for C/Chl. $a = 30$. They also show the seasonal change in relative numbers of diatoms and dinoflagellates; the latter are more abundant at higher temperatures.

Williams and Murdoch (1966) cite several other studies which show parallels between phytoplankton production in shallow marine waters and temperature over the seasons. The Danish

[3] Carlucci, A. F. 1972. Saturation constants for vitamin assimilation by phytoplankton. (Unpubl. manuscr.)

results are reviewed also by Steemann Nielsen (1960). Few of these earlier works included chlorophyll *a* measurements, however, and assimilation numbers are not reported.

Ichimura (1967) found a close relation between temperature and assimilation number for a station well within Tokyo Bay, but not at a station in deeper water. Nutrient limitation was postulated for the outer station.

Some of the values for assimilation number and its variation with temperature which can be conveniently summarized are provided in Table 6. One might have hoped, by comparison of the data with values expected from Figure 9, to check up on the quality of one's colleagues' work and to find some reported values outside the bounds of reasonable expectation. Happily, only one of the papers reviewed gave unrealistically high assimilation numbers and these were not repeated in subsequent studies by that author.

IMPLICATIONS FOR SIMULATION MODELS OF PHYTOPLANKTON PRODUCTION

As pointed out by Patten (1968) and others, mathematical models are usually designed to be accurate or alternatively, realistic, but seldom are both. It can be seen from the preceding discussion that attempts to compute photosynthetic rates from temperature would generally be inaccurate, and unrealistic as well, unless radiant energy and concentrations of essential nutrients were also considered. In the past, models of photosynthesis have often included a term for the maximum rate of photosynthesis at light saturation which is widely acknowledged to be temperature-dependent. In Steele's (1962) model P_{max} is a constant and is expressed in units "carbon assimilation rate per unit plant carbon"

TABLE 6.—Assimilation numbers measured in different ocean regions in comparison with maximum expected values taken from Figure 9. A similar table is given by Saijo and Ichimura (1962) for pelagic and coastal seawaters and lakes.

Region	Assimilation number (mg C/mg Chl./hr)				Temperature (°C)	Source
	Measured	Max. expected if C/Chl. =				
		30	60	90		
Cold Seas						
Antarctic	avg <2.5	1.0	2.0	3.0	−2-2	(1)
Subarctic North Pacific	0.4-2	1.4	2.7	4.0	2-6	(2)
North Atlantic	3.5	1.4	2.7	4.0	4-6	(3)
	3.5	1.7	3.4	5.1	9	(3)
	4	3.1	6.3	9.4	16	(3)
Upwelling Regions						
Peru Current	<7.5	4.6	9.2		17-20	(4)
Peru Current	5	4.6	9.2		[1](20)	(5)
S.W. Africa	<6.5	4.6	9.2		[1](20)	(6)
Cromwell Current	5.3	5.1	10.3		21	(7)
	10	8.0	16.0		25	(7)
Tropical Seas						
Madagascar	avg 3.8	8.0	16.0		[1](25)	(8)
Caribbean	avg 6.3a avg 3.7b	8.0	16.0		[1](25)	(9)
Tropical Pacific	avg 2.3a avg 1.5b	8.0	16.0		[1](25)	(9)
Off Puerto Rico	<13	8.0	16.0		[1](25)	(10)
Western Arabian Sea	avg 4.4	11.7	23.4		<28	(11)

[1] Assumed temperature.

Sources: (1) Saijo and Kawashima, 1964; El-Sayed and Mandelli, 1965; Mandelli and Burkholder, 1966; Horne et al. 1969; Bunt and Lee, 1970; (2) Biological station, Nanaimo (1970. Biological, chemical and physical data First Canadian Trans-Pacific Oceanographic Cruise March to May 1969. Fish. Res. Board Can., Manuscr. Rep. 1080, 92 p). (3) Steemann Nielsen and Hansen, 1959, for light-saturated rate; (5) Lorenzen, 1968, average over the euphotic zone; (7) Barber and Ryther, 1969, average over the euphotic zone; (8) Sournia, 1968; (9) Malone, 1971a. Values designated by "a" are for nanoplankton, "b" values for netplankton; (10) Burkholder, Burkholder, and Almodóvar, 1967; (11) Ryther and Menzel, 1965b, average for euphotic zone.

and is equivalent to a specific growth rate of about 1.1 doublings/day. Such a value would be appropriate for temperate waters, but probably not for polar or eutrophic tropical waters. But to make P_{max} a function of temperature would probably add unnecessary complexity for modeling purposes, although it would add realism. However, the use of constant values makes the model restrictive geographically (see, for example, Parsons and Anderson's, 1970, use of the model of Steele and Menzel, 1962, for the subarctic North Pacific).

A plant physiologist would perhaps prefer to approach modeling phytoplankton growth in the sea in as physiologically realistic way as possible and to let the computer handle the complexity. But it is questionable how realistically this can now be accomplished or what insight would thereby result.

Equation (1) of this paper can be considered a model of sorts and its apparent universality is appealing. Comparing its predictions as to growth rate and assimilation number with data from natural phytoplankton shows, moreover, the magnitude of difference between potential plant growth and reality, as it is now best estimated. The gulf between real and maximum expected values shows how significant are the other environmental factors which affect phytoplankton: radiant energy, nutrient concentrations, grazing, and mixing processes. All of these parameters have been successfully treated in models since the 1940's (see Patten's summary review, 1968; Parsons, Giovando, and LeBrasseur, 1966; Dugdale and Goering, 1967).

A physiologically realistic model might begin with a relation between temperature and maximum expected growth rate, as in Eppley and Sloan (1966). In that paper the variations in growth rate among species were rationalized by including the chlorophyll concentration per unit cell volume (a parameter not readily measurable in assemblages of mixed species, but susceptible to averaging). This parameter seemed also to compensate for the sun-shade alterations of phytoplankton photosynthesis when used to calculate radiant energy absorbed by a cell's pigments. However, the problem of daylength could not be adequately handled for species which grow faster with a few hours darkness each day than in continuous light.

None of the models proposed for primary productivity simulation has attempted to treat diel periodicity in the metabolic processes of phytoplankton. Nor is the alteration of chemical composition attendant to growth with limiting concentrations of nutrients or to variations with irradiance or temperature treated.

One suspects that the simple models now available can be satisfactory for describing the major features of regional phytoplankton production. Realistic physiological models will probably remain in the "special purpose" category for the insight of those familiar enough with the subject to use them as guide to their own research. Nevertheless, it is admitted, given the current popularity of modeling, that neither the reader nor the author may be able to resist for long the temptation to combine Equation (1) with a realistic function for nutrient assimilation rate vs. ambient concentration, a function for the dependence of μ and assimilation number upon light, and a suitable function for describing effects of mixing, in line with critical depth theory, and to try it with his favorite set of oceanic data.

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COMPARATIVE STUDY OF FOOD OF SKIPJACK AND YELLOWFIN TUNAS OFF THE COAST OF WEST AFRICA[1]

ALEXANDER DRAGOVICH AND THOMAS POTTHOFF[2]

ABSTRACT

Stomach contents of 711 skipjack tuna (*Katsuwonus pelamis*) and 132 yellowfin tuna (*Thunnus albacares*) captured in 1968 by live bait and trolling off the coast of West Africa were examined. A marked taxonomic similarity was noted between the organisms in the diets of the two tunas. Frequency of occurrence, displacement volume, and numbers of each food item identified are presented for each species of tuna. Fishes, mollusks, and crustaceans were the principal foods with fishes generally dominant. The most prominent fish families were Acanthuridae, Carangidae, Dactylopteridae, Gempylidae, Gonostomatidae, Lutjanidae, Mullidae, Priacanthidae, Scombridae, Serranidae, and Trichiuridae; mollusks were chiefly cephalopods (squids), and crustaceans consisted mostly of macrozooplankton. Juvenile tunas were present in the diet of both species of tunas.

Estimates of the size of forage organisms were primarily based on displacement volumes. In the majority of observations, food organisms displaced less than 1.0 ml and the displacement volumes of stomach contents varied for skipjack tuna from 0.1 to 20.0 ml and for yellowfin tuna from 0.1 to 60.0 ml.

Spearman's rank correlation analysis was used to test for a relation between the food type (in volume and frequency of occurrence) and the lengths of skipjack and yellowfin tunas. Significant correlations were noted between the size of skipjack tuna and both the volume and the frequency of occurrence of forage fish.

A comparison between the findings of our study and that of other food studies off the coast of West Africa showed greater taxonomic similarity in tuna forage when the studies were made in the same general area and that only several types of food were of primary importance in each given area. Seasonal changes in taxonomic composition of forage organisms were also discussed.

The method used to evaluate food organisms consisted of ranking the organisms according to their dispersal indices, abundance indices, and biomass contribution. Stomatopods, the amphipod *Phrosina semilunata*, Teuthoidea, Carangidae, Serranidae, and megalopal stages were most important constituents of food throughout the investigation area.

The principal surface tuna fishery in the tropical Atlantic Ocean is located off the coast of West Africa (Jones, 1969). One of the major tasks of the Southeast Fisheries Center, Miami Laboratory, has been the study of the biology and ecology of tunas and tunalike fishes in the tropical Atlantic Ocean. In view of the recognized importance of food as an ecological factor in the life history of tunas, one project of this investigation consisted of a study of the food and feeding habits of skipjack (*Katsuwonus pelamis*) and yellowfin (*Thunnus albacares*) tunas — the two predominant species in commercial catches in those waters.

We describe and compare the food of skipjack and yellowfin tunas and discuss the relative importance of different forage organisms. We compare our findings with those of other investigators working in the same general area. This

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information may be used to study the relationship between the distribution of food organisms and occurrence of tuna schools.

Most of the information up to 1969 on food of various tunas off the west coast of Africa may be found in the review of studies of tuna food in the Atlantic Ocean by Dragovich (1969). Dragovich (1970) also reported on the food of skipjack and yellowfin tunas off the west coast of Africa.

MATERIALS AND METHODS

Samples on which the present report is based were collected during February, March, April and September, October, November of 1968 on two cruises (UN6801 and UN6802) of the research vessel *Undaunted* of the Bureau of Commercial Fisheries (now National Marine Fisheries Service) (Figure 1). All tunas sampled for

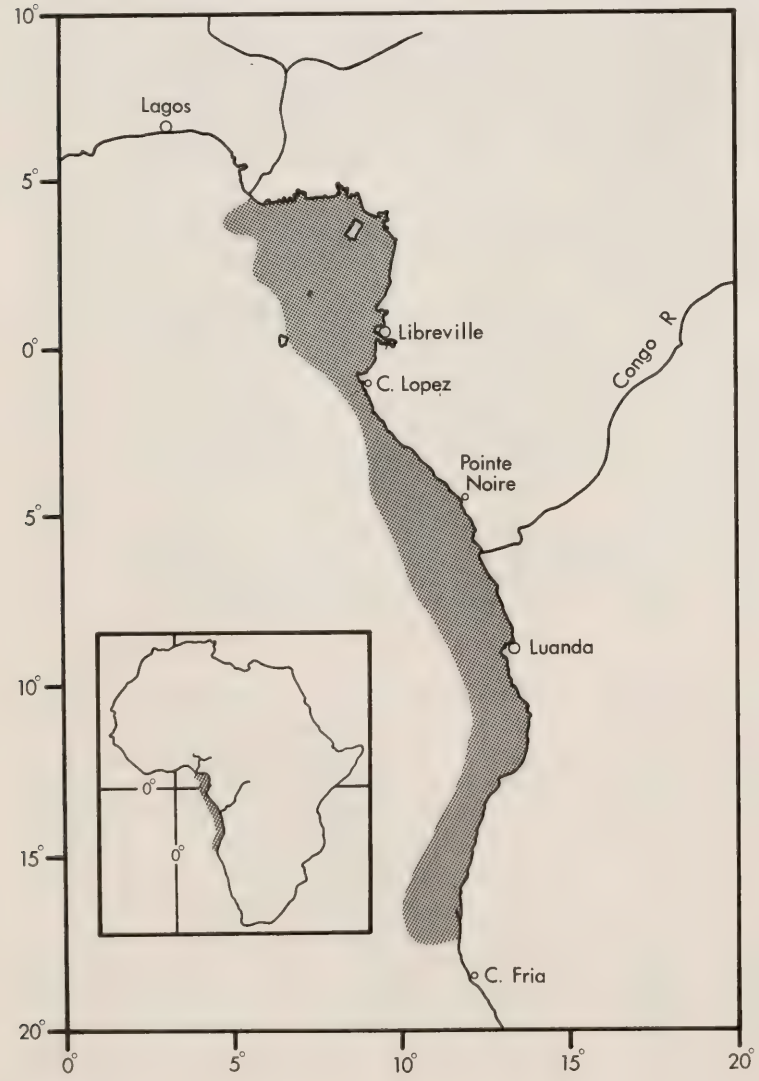

FIGURE 1.—Shaded area shows localities where stomachs of skipjack and yellowfin tunas were collected.

this study were caught by pole and line or by trolling (Table 1). A total of 711 stomachs from skipjack tuna and 132 from yellowfin tuna were examined. The skipjack tuna studied varied in fork length from 36 to 63 cm and the yellowfin tuna from 52 to 94 cm (Figure 2).

Sampling of catches for stomach samples was carried out as other requirements of the program and circumstances permitted. Immediately after completion of the morphometric work aboard the ship the stomachs were removed by opening the abdominal cavity and by severing them from the intestine and the esophagus. Each stomach was pierced in several places to allow

TABLE 1.—Distribution of skipjack and yellowfin tuna stomachs collected during 1968 from the eastern tropical Atlantic Ocean, identified by month, cruise, and method of capture.

February UN6801[1]		March UN6801		April UN6801		September UN6802[2]		October UN6802		November UN6802		Total		Method of capture
With food	Empty	With food	Empty	With food	Empty	With food	Empty	With food	Empty	With food	Empty	With food	Empty	
						Skipjack tuna								
		20	28	292	36	70	4	104	69	25	5	511	142	Live bait
41	8	3	3					3				47	11	Trolling
						Yellowfin tuna								
				67		24	4	18	1			109	5	Live bait
4		9	1	3						1		17	1	Trolling

[1] UN6801 = RV *Undaunted* 6801 cruise.
[2] UN6802 = RV *Undaunted* 6802 cruise.

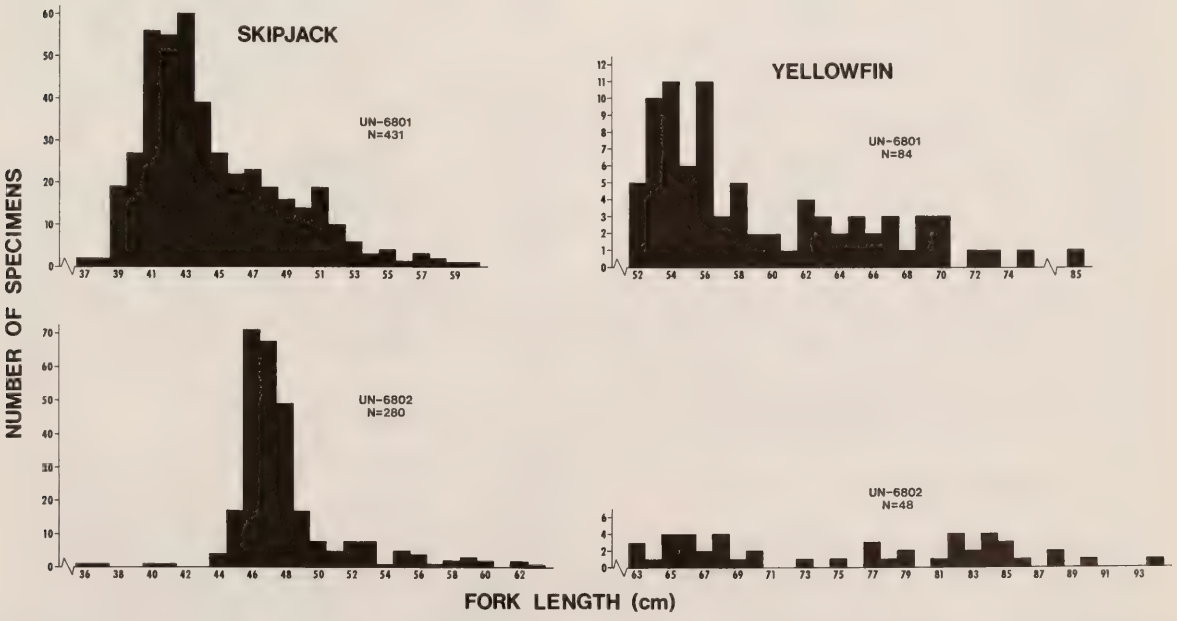

FIGURE 2.—Length-frequency distribution of skipjack tuna and yellowfin tunas from which stomachs were collected.

penetration of Formalin[3] and placed in a labeled polyethelene bag containing 10% Formalin.

In the laboratory the stomachs were first classified into those containing food and those that were empty. The stomach contents were then identified to the lowest possible taxonomic units which were subsequently sorted, counted, and their displacement volumes measured. Length measurements were taken of many forage organisms, particularly fishes. Bait fishes were found in some of the stomachs, but they were not considered as part of the regular diet of skipjack and yellowfin tunas; therefore, stomachs which contained only bait were considered empty. Stomachs that contained parasitic trematodes were also considered empty.

This study was no exception in regard to difficulties encountered in the identification of forage organisms (Dragovich, 1969). In numerous instances the identification of ingested fishes, particularly juvenile tunas, was made from vertebrae using methods employed by Potthoff and Richards (1970). Cephalopod identification was particularly difficult since many diagnostic external characters usually are the first destroyed during digestion.

The following methods of analysis were used: 1) the volumetric method—the individual volume of each taxon and the total aggregate volume of broad taxonomic groups, 2) frequency of occurrence method—the frequency of occurrence of a food item and of broad taxonomic groups, and 3) numerical method—number of individuals in the same taxonomic group.

Spearman's rank correlation test, χ^2 test of homogeneity, and paired t-test of difference between the means were used. A method consisting of ranking of food organisms according to their geographic distribution, relative abundance, and biomass was also employed.

COMPOSITION OF FOOD

Fishes, crustaceans, and cephalopods were the three principal food categories found in stomachs of both skipjack and yellowfin tunas (Figure 3). Food items that do not fall into these three categories consisted of mollusks other than cephalopods, salps, polychaetes, and siphonophores. Other mollusks and salps were found in both species of tunas; polychaetes and siphonophores were present only in stomachs of skipjack tunas. A checklist of all food items, number of organisms, frequency of occurrence, displacement volumes, and length measurements of some organisms are presented according to the cruises in Appendix Tables 1 to 4. Fishes were represented in the diet of skipjack and yellowfin tunas by 90 different taxa, crustaceans by 45, and mollusks by 24.

The percentage composition of five food categories in terms of number, volume, and frequency of occurrence is shown in Figure 3. Fish was the dominant food item by volume for both species of tunas, except for yellowfin tuna captured during UN6802, when cephalopods were dominant. Fish occurred most frequently in the diet of both species of tunas sampled during UN6801; however, crustaceans occurred most often in the collections from UN6802. In the diet of yellowfin tuna, fishes were numerically the most important food items during both cruises; in the diet of skipjack tuna, fishes were the most important by numbers during UN6801, but crustaceans were most numerous during UN6802.

The group of forage organisms classed as other mollusks consisted primarily of pteropods and heteropods. Salps, polychaetes, and siphonophores were the principal components of the group of forage organisms classed as miscellaneous—this group was not prominent by volume, frequency of occurrence, or by numbers.

FISHES

Fishes utilized as food consisted mainly of postlarval and juvenile forms of pelagic and reef fishes. Some adult fishes, primarily *Vinciguerria nimbaria*, were also present in the diet of both species of tuna. Although fishes were represented by a larger number of families, only a few families were important in terms of volume, frequency of occurrence, and numbers.

[3] Use of trade names does not imply endorsement by the National Marine Fisheries Service.

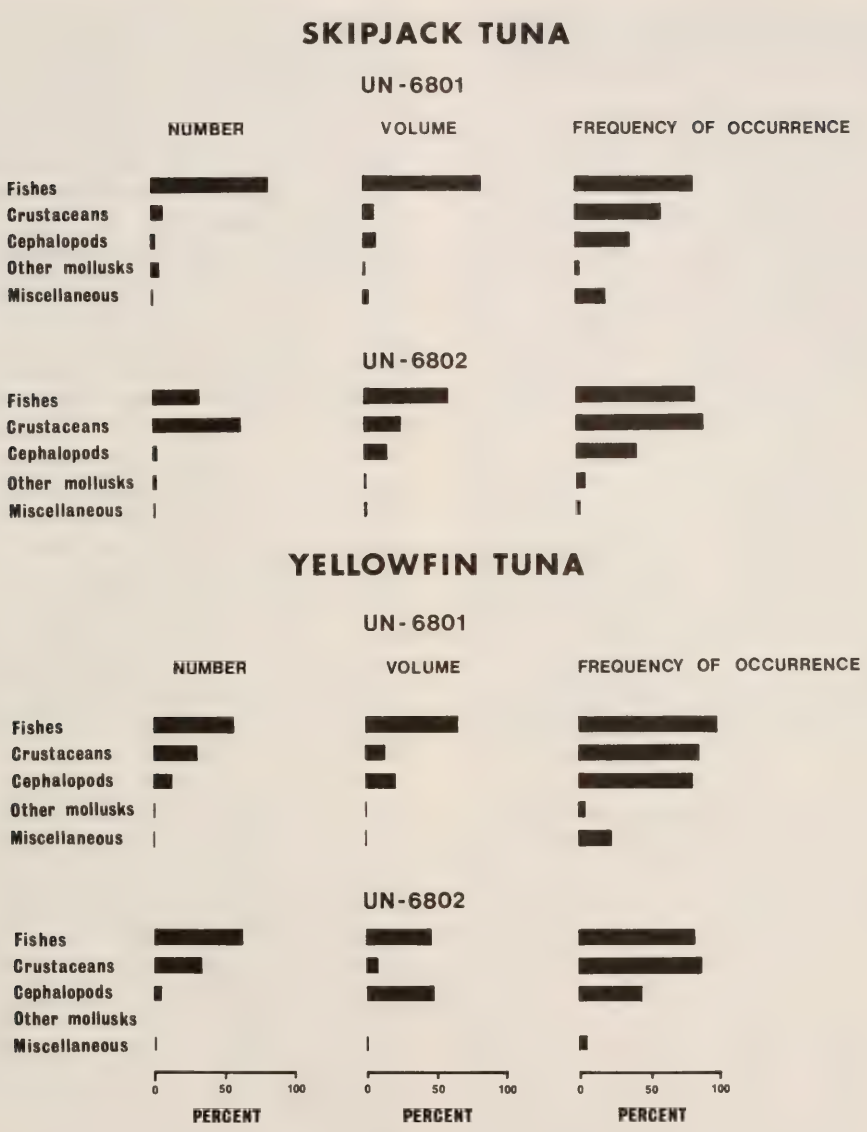

FIGURE 3.—Percentage of total food (by five categories) in stomachs of skipjack and yellowfin tunas captured during cruises UN6801 and UN6802 off the west coast of Africa. Food items are represented in terms of numbers, volumes, and frequency of occurrence.

For UN6801, fish families Acanthuridae, Carangidae, Dactylopteridae, Gempylidae, Gonostomatidae, Lutjanidae, Mullidae, Priacanthidae, Scombridae, and Serranidae ranked high in terms of volume and frequency of occurrence for both species of tunas. Owing to the large numbers of *V. nimbaria* in the diet of both species of tunas, the family Gonostomatidae was the most important forage item for both species in terms of volume. In the diet of skipjack tuna,

important contributors by volume were Gonostomatidae, 44.7%; Engraulidae, 8.9%; Mullidae, 7.9%; Gempylidae, 2.7%; Serranidae, 2.5%; Lutjanidae, 2.0%; Scombridae, 1.6%; Carangidae, 1.6%; and Priacanthidae, 1.5%. Important contributors by volume to the diet of yellowfin tuna were Gonostomatidae, 22.1%; Mullidae, 14.8%; Tetragonuridae, 6.3%; Carangidae, 3.8%; Paralepididae, 1.5%; Priacanthidae, 1.2%; and Scombridae, 1.0%. The remaining fish families contributed less than 1% per family for both species of tunas. The high volumetric contribution by the family Tetragonuridae was due to the large size of only four *Tetragonurus cuvieri*, which were found in a single stomach of a yellowfin tuna.

During UN6802 most important fish families by volume and by frequency of occurrence were Carangidae, Gempylidae, Paralepididae, Scombridae, and Trichiuridae. Serranidae and Scorpaenidae were prominent in the diet of skipjack tuna, but entirely absent in the diet of yellowfin tuna. Important contributors by volume in the diet of skipjack tuna were Paralepididae, 28.4%; Percoidei, 8.6%; Carangidae, 3.1%; Serranidae, 1.5%; Trichiuridae, 1.4%; Gempylidae, 1.3%; and Scombridae, 1.2%. In the diet of yellowfin tuna important contributors by volume were Exocoetidae, 9.6%; Alepisauridae, 5.6%; Carangidae, 2.7%; Trachypteridae, 2.6%; Scombridae, 2.5%; and Percoidei, 1.4%. The remaining fish families and suborders in the diet of both species of tunas contributed less than 1% per taxon in terms of volume. The relatively high contribution by the families Exocoetidae and Alepisauridae was due to the large volumes of only three forage fish (Appendix Table 4). From our data we see that some of the prominent forage fish families for both species of tunas were common to both cruises and that others were important during only one cruise (Appendix Tables 1-4).

CRUSTACEANS

As shown in previous publications (Dragovich, 1969, 1970), crustaceans, because of their high numbers and high frequency of occurrence, were important components of tuna food. Crustaceans found in tuna stomachs during both cruises were similar. The majority were larval stomatopods, hyperiid amphipods, and different types of megalopae or their equivalents. The highest number (32) of taxa was noted in the diet of skipjack tuna during UN6801, while in the diet of yellowfin tuna for the same cruise, 20 different taxa were identified—16 of these were common in the diet of both species of tunas. During UN6802, 22 different taxa were identified in the diet of skipjack tuna and 10 in the diet of yellowfin tuna—7 were common to both species of tuna. Stomatopods were not identified further than order. *Phronima sedentaria*, *Phrosina semilunata*, and *Brachyscellus* spp. were the most common amphipods in both tunas for both cruises. Megalopal stages probably consisted of many species, but due to the lack of taxonomic literature, they were not identified further than class or family.

A variety of anomurans and caridean shrimp were consumed by both species of tunas. *Dardanus pectinatus* (Glaucothoë) was the most important anomuran for both tunas during both cruises. Carideans were more prominent during UN6801 than during UN6802.

Euphausia hanseni was eaten by both tunas during UN6801. During UN6802, *E. hanseni* occurred in high numbers in the diet of skipjack tuna but was entirely absent in the food of yellowfin tuna. Since *E. hanseni* are of minute size, they were probably accidentally ingested or the skipjack tuna were filter feeding. The same explanation may be applied to other organisms of similar size found in the stomachs of both species of tunas, for example, copepods and isopods. Another explanation is that some of the euphausiids, copepods, or isopods could be the remains of stomach contents of other fishes ingested by tunas.

Phyllosoma occurred in low numbers in the diet of both species during both cruises. The identified forms were *Panulirus rissoni*, *Scyllarus arctus*, *Scyllarus* sp., and *Scyllaridea* sp.

MOLLUSKS

Cephalopods formed the bulk of the molluscan food of both species of tunas during both cruises.

Teuthoidea (squid) were the most important by volume and by frequency of occurrence in the diet of both species. Most of the squid belong to the family Ommastrephidae. Among identified omasterphids, *Ornithoteuthis antillarum* was most frequently encountered. This species was especially numerous in the food of skipjack tuna during UN6802. Octopoda were less numerous and occurred with less frequency than Teuthoidea. The displacement volume of some of the Octopoda (*Argonauta argo* and *A.* sp.) was very large. Five specimens of *A. argo* consumed by yellowfin tuna during UN6802 displaced 165.5 ml—more than all other mollusks combined for that cruise or all the fishes for that cruise (Appendix Table 4).

Among other mollusks, pteropods and heteropods were found in the stomachs of skipjack tuna during both cruises. They were absent in the food of yellowfin tuna during UN6802 and occurred only in two stomachs during UN6801. A heteropod, *Cavolinia longirostris*, occurred in high numbers in the diet of skipjack tuna during UN6801. In terms of volume, both of these mollusks were of minor importance.

JUVENILE TUNAS AS FOOD OF SKIPJACK AND YELLOWFIN TUNAS

Knowledge on the distribution and abundance of juvenile tunas and tunalike fishes is very limited because existing collection methods for juveniles are inadequate. This information is very important, however, as an aid in identifying spawning seasons and areas of tunas. One of the major sources of juvenile tunas is from stomachs of adult tunas. Juvenile tunas and tunalike fishes were present in the diet of both species of tunas sampled on both cruises. As many as 20 juvenile tunas were found in a single tuna stomach. The most frequently encountered and the most numerous juvenile tunas were *Auxis* spp. and little tunny (*Euthynnus alletteratus*) (Table 2). Specimens of *Auxis* spp. were found in both species of tunas during both cruises. Specimens of *E. alletteratus* were present in the diet of both species of tunas, but only during UN6801. All the remaining species of juvenile tunas occurred infrequently in small numbers. *Katsuwonus pelamis* and *Thunnus*

TABLE 2.—Occurrence of juvenile scombrids in the stomachs of skipjack and yellowfin tunas during cruises UN6801 and UN6802.

	Total number	Standard length (mm)		Number of juveniles in a single stomach	Frequency of occurrence		Displacement volumes	
		Range	Mean		Number	Percent	ml	Percent
Skipjack tuna UN6801								
Unidentified Scombridae	4	--	--	1, 2	3	0.8	0.5	<0.1
Auxis spp.	53	12-37	29	1, 2, 3, 4, 9	29	8.1	9.5	0.3
Euthynnus alletteratus	120	10-68	29	1, 2, 3, 4, 5, 10	66	18.5	28.1	1.0
Katsuwonus pelamis	2	20-32	26	1	2	0.6	0.3	0.3
Thunnus spp.	2	34-47	41	1	2	0.6	1.4	<0.1
Skipjack tuna UN6802								
Auxis spp.	33	15-63	31	1, 6, 16	10	5.0	8.6	0.9
Sarda sarda	4	25-43	34	1	4	2.0	2.3	0.2
Scomber japonicus	1	--	40	1	1	0.5	1.3	0.1
Yellowfin tuna UN6801								
Auxis spp.	7	12-50	22	1, 2	5	6.0	1.4	<0.1
Euthynnus alletteratus	58	11-70	33	1, 2, 3, 4, 5, 6, 8	21	25.3	18.0	0.7
Katsuwonus pelamis	1	38	38	1	1	1.2	0.2	<0.1
Thunnus spp.	3	29-40	36	1	3	3.6	0.8	<0.1
Yellowfin tuna UN6802								
Unidentified Scombridae	15	--	--	1, 3, 8	6	14.0	0.8	0.2
Auxis spp.	53	15-34	22	1, 2, 4, 7, 20	11	25.6	7.4	2.1
Sarda sarda	4	15-21	18	1, 3	2	4.7	0.5	0.1
Scomber japonicus	1	--	28	1	1	2.3	0.1	<0.1

spp. were found in the stomachs of both species of tunas, but only during UN6801. *Sarda sarda* and *Scomber japonicus* were also found in both skipjack and yellowfin tunas, but only during UN6802.

The presence of juvenile tunas in the diet of skipjack and yellowfin tunas in various parts of the Atlantic Ocean has been reported by Dragovich (1969, 1970). Presence of *Auxis* spp. and *Scomber* sp. in the diet of yellowfin tuna from east African waters was noted by Williams (1966). Suarez Caabro and Duarte Bello (1961) noted juvenile blackfin tuna (*Thunnus atlanticus*) (5-150 mm fork length) and skipjack tuna (35-145 mm fork length) in the stomachs of skipjack tuna from the Caribbean Sea. Presence of juvenile tunas in the diet of adult tunas has been frequently observed in food studies in the Pacific Ocean (Reintjes and King, 1953; King and Ikehara, 1956; Alverson, 1963; Nakamura, 1965).

COMPARISON OF FOOD OF SKIPJACK AND YELLOWFIN TUNAS

As in a previous study by Dragovich (1970), our data show a marked taxonomic similarity of items in the diet of skipjack and yellowfin tunas for the investigation area as a whole (Appendix Tables 1-4). We also compared the taxonomic composition of forage organisms at the two locations where skipjack and yellowfin tunas were caught together in a mixed school. For those locations we performed χ^2 tests of homogeneity on the ratio of fish to total volume of food. The first test indicated that the percentage of fish consumed differs between the two locations ($\chi^2 = 6.74$; 1 *df*; $P < 0.1$) possibly reflecting differences in forage-at-large composition, times of day, size frequency of tuna, etc. Within-area difference in percent fish between yellowfin and skipjack tunas was significant in only one area ($\chi^2 = 62.51$; 1 *df*; $P < 0.01$).

TABLE 3.—The distribution of displacement volumes of individual forage organisms collected during the cruises of UN6801 and UN6802.

Food item	Total range of displacement volumes (ml)	Displacement volumes in 90% of observations
	Skipjack tuna	
Fish	0.1- 8.2	0.1-0.3
Crustaceans	0.1- 1.2	0.1
Cephalopods	0.1- 6.5	0.1-1.6
Other mollusks	0.1- 0.4	0.1
Salps	0.1- 3.5	0.1-0.7
	Yellowfin tuna	
Fish	0.1-55.0	0.1-0.5
Crustaceans	0.1- 1.0	0.1
Cephalopods	0.1-50.5	0.1-0.7
Salps	0.1	0.1

VARIATION IN FOOD AS RELATED TO SIZE OF TUNAS AND VOLUME OF STOMACH CONTENTS

The foods of skipjack and yellowfin tunas in the present study consisted principally of relatively small organisms, based on their displacement volumes (Table 3). The consumption of organisms of comparable size in similar proportions by skipjack and yellowfin tunas has also been observed by other investigators (Reintjes and King, 1953; King and Ikehara, 1956; Nakamura, 1965; Williams, 1966; Dragovich, 1970).

To observe the differences in consumption of food by volume and frequency of occurrence of the three major food categories as related to size of tunas, skipjack and yellowfin tunas were separated into 20 mm and 30 mm length intervals respectively (Figure 4). Spearman's rank correlation analysis (Steel and Torrie, 1960:409) was used to see if the volumes and frequency of occurrence of the two dominant forage food items (fishes and crustaceans) in the diet of skipjack and yellowfin tunas were correlated with the size of tunas. Significant correlations in the length-food data were noted between the size of skipjack tuna and percentage volume of fish forage (r_s 0.576, 11 *df*, $P < 0.05$) and percentage of occurrence of forage fish (r_s 0.565, 11 *df*, $P < 0.05$), suggesting that as the size of tuna increased, the percentage consumption of fish by volume and by frequency of occurrence increased.

It is generally recognized that the amount and quality of food found in the stomach of tunas

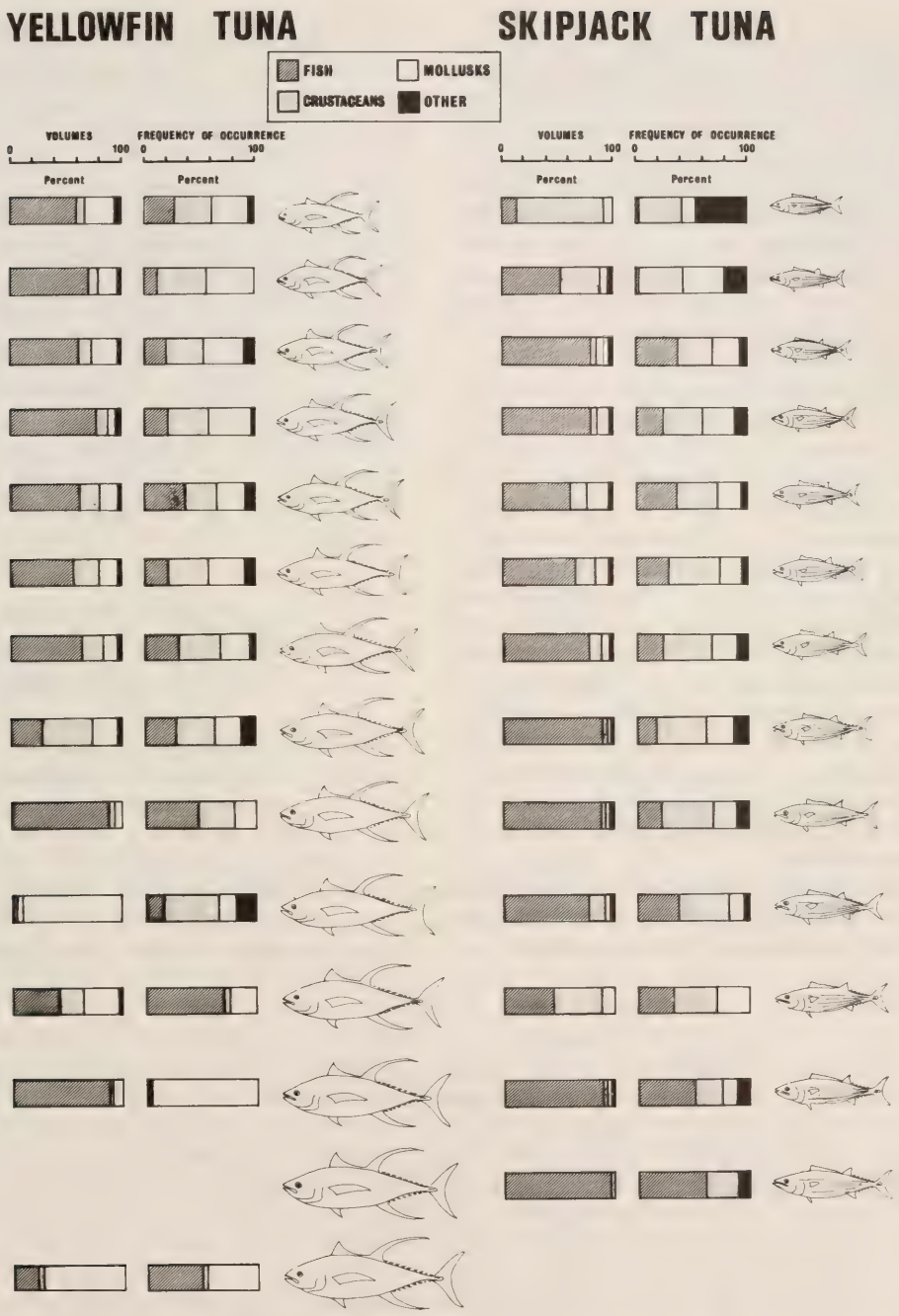

FIGURE 4.—The distribution of volumes and frequencies of occurrence of the major food categories (fish, crustaceans, mollusks, and miscellaneous) at various sizes of skipjack and yellowfin tunas off the west coast of Africa, The sizes of skipjack range from 370 mm to 610 mm (intervals 20 mm); the sizes of yellowfin tuna range from 520 mm to 910 mm (intervals 30 mm).

are important in studies concerned with energy that is converted into caloric equivalents of energy utilized for growth. We have the information only on the volumes of the stomach contents. This information may be of interest to the investigators concerned with energy budgets of tunas and with studies on transfers of energy within the food web. In our study, in the majority of observations, the displacement volumes of the total stomach contents of skipjack and yellowfin tunas varied from 0.1 to 20.0 ml and from 0.1 to 60.0 ml, respectively (Table 4). Information on the volumes of stomach contents of tunas in the Atlantic Ocean is found only in a limited number of investigations, as cited in the review of studies of tuna food in the Atlantic Ocean by Dragovich (1969). Dragovich (1970) noted volumes of stomachs of less than 20 ml in 75% of skipjack tuna sampled and in 85% of yellowfin tuna. Volumes of stomach contents of yellowfin tuna caught by longline off the coast of east Africa (Williams, 1966) were generally higher than those in our study. The majority of the volumes measured by Williams fell within a range of 3.0 to 499.9 cc. Higher volumes of stomach contents observed by Williams may be partially explained by the fact that tunas caught on longline are usually larger than fishes caught by surface methods.

To determine the relation between the volume of stomach contents and body weight of skipjack and yellowfin tunas, we have assumed that 1.0 ml of stomach contents is equivalent to 1.0 g. Comparisons on this basis were made between the estimated weight of the stomach contents and the body weights of tunas. Our calculations have shown that the total volume of stomach contents for both species of tunas in almost all observations was well below 1.0% of the body weight. This observation is in agreement with the findings by Dragovich (1970). The results of these calculations suggest that there was little difference in the total amount of food found in the stomachs of both species of tunas as related to the body weight. Possible explanations for such low volumes of stomach contents may be rapid digestion of food, long periods between the feedings, scarcity of food, and the fact that most of the forage organisms are very small macrozooplankton.

SEASONAL CHANGES IN TAXONOMIC COMPOSITION OF FORAGE ORGANISMS

Cruise UN6801 took place in the Gulf of Guinea during what is sometimes called the "warm" season (February, March, and April) and UN6802 during the "cool" season (September, October, and November). Berrit (1961) in his study on seasonal variations of oceanographic conditions introduced these terms. Results on studies by Sund and Richards (1967)

TABLE 4.—Distribution of the volumes of total stomach contents in 711 skipjack tuna and 132 yellowfin tuna stomachs. The data were collected during cruises UN6801 and UN6802.

Volume of stomach contents (ml)	Skipjack tuna			Yellowfin tuna		
	Number of stomachs	Percentage	Accumulated percentage	Number of stomachs	Percentage	Accumulated percentage
Empty	153	21.5	21.5	6	4.5	4.5
0.1-0.5	127	17.9	39.4	8	6.1	10.6
0.6-1.0	70	9.8	49.2	7	5.3	15.9
1.1-1.9	69	9.7	58.9	9	6.8	22.7
2.0-2.9	46	6.5	65.4	10	7.6	30.3
3.0-3.9	37	5.2	70.6	5	3.8	34.1
4.0-4.9	32	4.5	75.1	10	7.6	41.7
5.0-10.0	80	11.2	86.3	15	11.4	53.1
10.1-20.0	63	8.9	95.2	15	11.4	64.5
20.1-60.0	24	3.4	98.6	34	25.7	90.2
60.1-100.0	6	0.8	99.4	12	9.1	99.3
100.1-200.0	4	0.6	100.0	1	0.7	100.0

on the differences in the occurrence of forage organisms of skipjack and yellowfin tunas in the Gulf of Guinea between these two seasons are compared with ours.

In our study, the fish families present in the diet of both species of tunas only during the "warm" period were Mullidae, Dactylopteridae, Gonostomatidae, and Engraulidae. In the study of Sund and Richards (1967), Dactylopteridae were also present during the "warm" season only. A number of crustacean taxa were present in our study only during the "warm" season and absent during the "cool" season. Grapsidae (megalopal stages), *Petrochirus* sp. and *Streetia challengeri*, were found only during the "warm" period and absent during the "cool" period. Other prominent crustaceans observed by us in stomachs of both species of tunas only during the "cool" period were *Vibilia armata, Scyllarides* sp., *Scyllarus* sp., and *S. arctus*. Some of the crustaceans (*Phronima sedentaria, Phrosina semilunata, Euphausia* sp.) occurred only in one season in the observations of Sund and Richards (1967), whereas we observed them in both seasons. More extensive collections are needed before any final evaluation is made in regard to the significance of the occurrence of these organisms during different seasons.

EVALUATION OF FOOD ORGANISMS

In selecting the most important food organisms in a given area, many variables have to be considered. Reintjes and King (1953) stated that food items that rank high in number, high in volume, and high in frequency of occurrence are important foods—at the time and in the area sampled. Using these criteria plus the geographic distribution in evaluation of food organisms of both species of tunas, we have calculated dispersal and abundance indices and mean displacement volumes for each food taxon and ranked them accordingly.

The entire investigation area was divided into 27 one-degree squares. If a taxon was present in one square it was assigned a value of one. Using the data from both cruises and for both species of tunas combined, the number of occurrences of each taxon in 27 squares was divided by the number of squares—the quotient was called the dispersal index. An abundance index was calculated by dividing the total number of individuals in each taxon by the total number of all organisms. An approximation of biomass of each food item was represented by the mean displacement volume. The mean displacement volume of food items represented in Figure 5 varied from 0.1 to 0.7 ml.

Since a large number of taxa are represented, we have selected the 32 taxa with the highest dispersal and abundance indices and presented them in a descending order of magnitude (Figure 5). *Vinciguerria nimbaria* and *Anchoviella guineensis*, although with low dispersal indices, were included in the diagram because of their high abundance indices. From Figure 5 it is obvious that Stomatopoda, *Phrosina semilunata*, Teuthoidea, Carangidae, Serranidae, and megalopal stages were the most important identifiable food items throughout the investigation area while *V. nimbaria, Euphausia hanseni*, and *A. guineensis* were of great local importance.

In the evaluation of forage organisms by the present method we consider the geographic dispersal of food organisms to be the most important criterion for the survival of skipjack and yellowfin tunas, particularly since these tunas are migratory and widely distributed. In our study the tuna forage organisms were both widely distributed and abundant in the area of sampling as indicated in Figure 5. High abundance indices were usually associated with high dispersal indices. Thus these food organisms may be considered to be important in the food chain of skipjack and yellowfin tunas for the given time and area.

The disadvantage of the method is that the estimated geographic distribution of forage taxa as calculated from stomach contents may not represent the true distribution. The only other information nearest to the natural distribution of certain forage organisms found in our study was obtained from zooplankton double oblique tows which were made at about the same time of the capture of tunas from which stomach samples were taken. The preliminary analysis of the composition of zooplankton from these

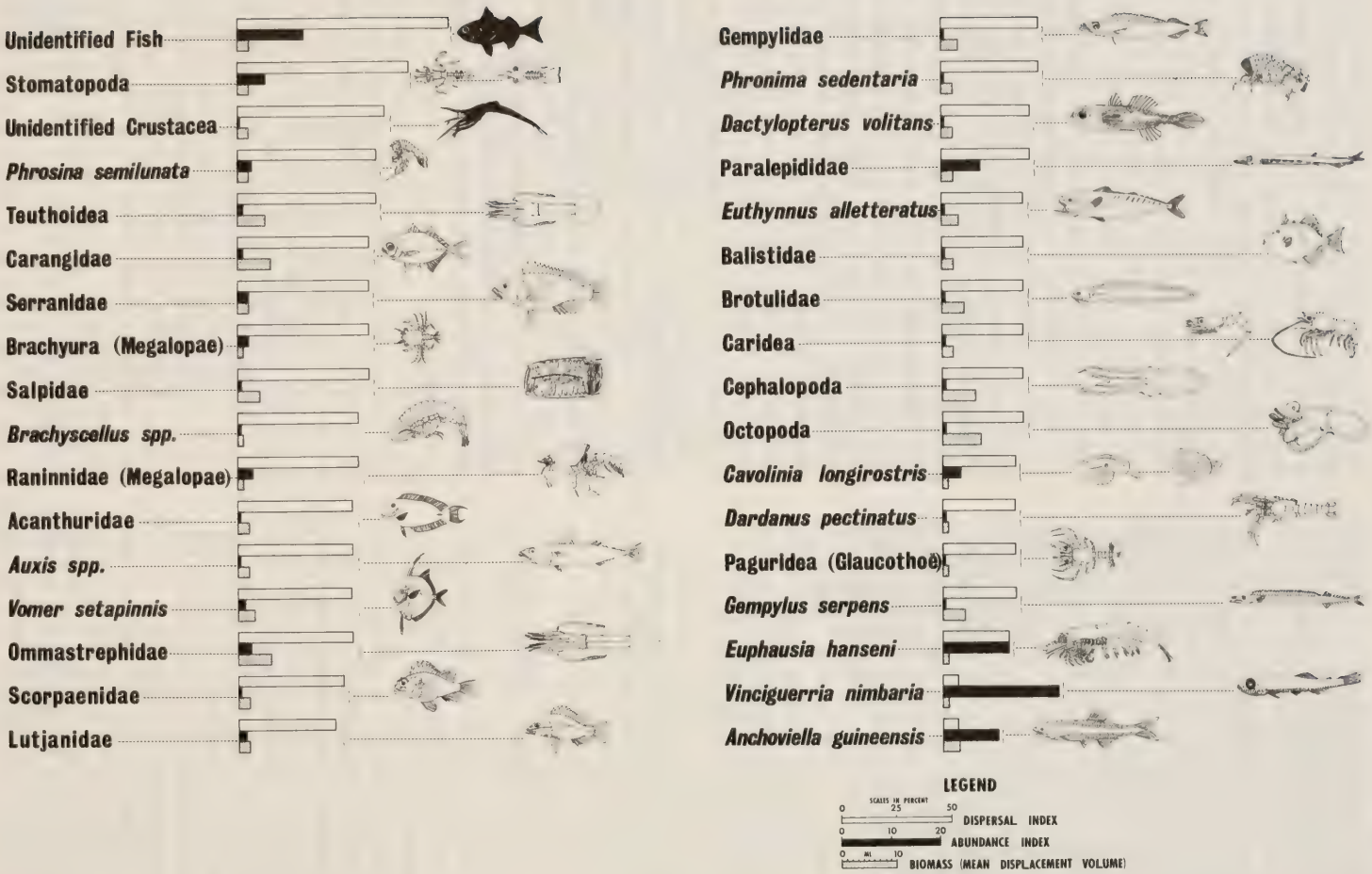

FIGURE 5.—The dispersal and abundance indices and biomass of forage organisms of skipjack and yellowfin tunas off the west coast of Africa. Dispersal and abundance indices expressed in percent. The biomass expressed in milliliters.

plankton samples showed that the major constituents were copepods and arrowworms. Arrowworms were entirely absent in the diet of both species of tunas. Although copepods were present in the stomachs of a few skipjack tunas, they may have been remains of the stomach contents of the ingested fishes. Among the minor constituents of zooplankton, 60 species and 10 genera of amphipods and 20 species and 3 genera of euphausiids were present in the plankton tows. Although all of the amphipods and euphausiids found in the tuna stomachs were also present in the plankton tows, their number represented only a small fraction of the number of taxa found in the plankton tows, thus suggesting selectivity in feeding of skipjack and yellowfin tunas. Our findings support those of Blackburn (1965), who stated that no species of tuna consumes all the species of net-caught micronekton or zooplankton.

COMPARISONS WITH RESULTS OF OTHER INVESTIGATORS

Investigations concerned with the food of skipjack and yellowfin tunas off the west coast of Africa are numerous (Postel, 1954, 1955a, 1955b; Marchal, 1959; de Jager, de V. Nepgen, and van Wyk, 1963; Penrith, 1963; Sund and Richards, 1967; de V. Nepgen, 1970; and Dragovich, 1970). Reliable qualitative comparisons of tuna forage between different studies are difficult because identification of organisms is usually incomplete. Quantitative comparisons between various studies of tuna forage usually consist of comparisons between the major food categories (fishes, crustaceans, and cephalopods). The nearest areas of the Atlantic Ocean to our investigation area for which valid comparisons can be made were investigated by Marchal (1959), Sund and Richards (1967), and Dragovich (1970).

The diet of yellowfin and skipjack tunas in the Gulf of Guinea was studied by Marchal (1959) and Sund and Richards (1967), respectively. From a long list of forage organisms presented by Marchal only several fishes (*Vomer setapinnis, Euthynnus alletteratus, Sternoptyx diaphana, Hyppocampus* sp., *Ophidion barbatum,* Brotulidae, Chiasmodontidae), a few crustaceans (Stomatopoda, *Heterocarpus ensifer,* Glaucothoë, megalopae (Brachyura)), and salps were common to both studies. All fish families in the diet of yellowfin tuna and skipjack tuna observed by Sund and Richards (1967) were also observed by us. The differences in the composition of tuna food between our study and that of Sund and Richards were on generic and specific levels except for cephalopods, where our findings differed entirely.

A striking similarity in the food of skipjack and yellowfin tunas was observed between our study and that of Dragovich (1970). Skipjack and yellowfin tunas in the study by Dragovich were captured off the coast of West Africa from Sierra Leone to Angola. All forage-fish families (21) in the diet of skipjack tuna noted by Dragovich were also observed by us. The most prominent fish families (Carangidae, Scombridae, Gempylidae) in terms of volume of frequency of occurrence observed by Dragovich were equally important in our study. We found the same groups of crustaceans as Dragovich. In the cephalopod diet ommastrephids were the principal food in both studies.

Postel (1955a) examined contents of stomachs of yellowfin tuna caught off the coast of Senegal. Of 30 species and 7 genera of fish and 12 cephalopod taxa listed by Postel, only *Euthynnus alletteratus, Katsuwonus pelamis, Sphyraena* sp., *Cranchia scabra,* and *Argonauta* sp. were observed by us. None of the identified species and genera of crustaceans by Postel was observed by us. The pronounced taxonomic differences of forage between our study and that of Postel may be partially explained by the different oceanographic regime off the coast of Senegal.

Postel (1955b), in his report on *Katsuwonus pelamis* off Cape Verde Islands, identified *Sardinella aurita, S.* sp., Myctophidae, *Hemiramphus* sp., *Hyporamphus* sp., *Gephyroberyx darwini, Scomber colias, Aphanopus* sp., and Mullidae in the diet of this tuna. Myctophidae and Mullidae were also observed by us in the diet of skipjack tuna. From cephalopods, only *Illex illecebrosus coindeti* was listed; this species was not identified in the diet of skipjack by us.

De Jager, de V. Nepgen, and van Wyk (1963), de V. Nepgen (1970), and Penrith (1963) reported that the food of yellowfin tuna caught off South Africa consisted mainly of fish. De Jager, de V. Nepgen, and van Wyk stated that lanternfish and anchovies occurred more frequently in the diet of yellowfin tuna than in the diet of other species of tunas; crab megalopae were by far the highest ranking crustaceans. Fish in de V. Nepgen's (1970) study consisted chiefly of garfish, lanternfish, and mackerel (*Scomber japonicus*). Most of the forage fishes reported by Penrith (1963) were surface fishes (*Scomberesox saurus, Coryphaena hippurus,* juvenile Bramidae). Among crustaceans Penrith (1963) found that yellowfin tuna fed chiefly on the deep-living prawn, *Funchalia woodwardii.* Megalopae also played an important role in the food of yellowfin tuna and were more important than amphipods. Mollusks consisted of unidentified cephalopods (squid), heteropods, and pteropods. In our study lanternfish and mackerel were unimportant as forage for yellowfin and skipjack tunas, and anchovies were not eaten by yellowfin tuna but occurred in great numbers in the diet of skipjack tuna; megalopae were among the highest ranking crustaceans. From a high number of forage fishes listed by Penrith (1963) only unidentified Carangidae, *Naucrates ductor,* unidentified Priacanthidae, *Priacanthus* sp., Acanthuridae, Scombridae, Balistidae, Blennidae, Bramidae, Coryphaenidae, *Coryphaena hippurus,* and Syngnathidae were also observed by us. Crustaceans common to Penrith's and our study were stomatopods, amphipods (*Phronima sedentaria, Phrosina semilunata*), and megalopae (Brachyura). Molluscan food for the most part was different between our study and that of Penrith (1963).

On the basis of the studies discussed in this section, it is evident that skipjack and yellowfin tunas consume a great variety of forage organisms. Fish, cephalopods, and crustaceans were the principal foods of both species of tunas in all investigations. The similarity in regard to the taxonomic composition of forage between different studies was greater when the investigations were made in the same general area. In each given area, only several types of food were important. Although occasionally bottom organisms were found in the diet of a skipjack and particularly yellowfin tunas, both of these species primarily feed on juvenile pelagic organisms.

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APPENDIX TABLE 1.—List of forage organisms found in stomachs from 356 skipjack tunas, collected off the west coast of Africa during UN6801. Number of organisms, frequency of occurrence, and percentage of total volume are given for each taxon. Size ranges and mean sizes are given only for certain forage fishes. Fishes are listed in decreasing order of frequency of occurrence by families; crustaceans, mollusks, and miscellaneous groups are listed by broad categories.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Fishes:							
Unidentifiable	1,912	229	64.3	179.5	6.5	7-57	19
Carangidae							
Vomer setapinnis	174	88	24.7	25.3	0.9	8-33	15
Decapterus spp.	6	5	1.4	1.5	<0.1	20-43	25
Unidentified Carangidae	85	54	15.2	14.8	0.5	6-46	20
Scombridae							
Euthynnus alletteratus	120	66	18.5	28.1	1.0	10-68	29
Auxis spp.	53	29	8.1	9.5	0.3	12-37	29
Katsuwonus pelamis	2	2	0.6	0.3	<0.1	20-32	26
Thunnus spp.	2	2	0.6	1.4	<0.1	34-47	41
Unidentified Scombridae	4	3	0.8	0.5	<0.1		
Gempylidae							
Gempylus serpens	48	28	7.9	34.3	1.2	18-216	70
Nealotus tripes	13	11	3.1	10.2	0.4	20-85	51
Promethichthys prometheus	8	7	2.0	3.0	0.1	24-65	45
Nesiarchus nasutus	1	1	0.3	0.1	<0.1		
Unidentified Gempylidae	89	54	15.2	26.4	0.9	18-83	57
Mullidae							
Pseudupeneus prayensis	278	80	22.5	196.8	7.1	32-49	42
Unidentified Mullidae	45	18	5.1	22.1	0.8	40-48	44
Priacanthidae							
Priacanthus spp.	84	50	14.0	23.6	0.9	9-31	21
Priacanthus arenatus	24	14	3.9	15.8	0.6	22-33	30
Lutjanidae							
Unidentified Lutjanidae	392	64	18.0	55.3	2.0	10-36	18
Serranidae							
Unidentified Serranidae	395	62	17.4	69.8	2.5	11-28	20
Acanthuridae							
Acanthurus monroviae	21	11	3.1	10.1	0.4	13-30	24
Unidentified Acanthuridae	65	40	11.2	13.8	0.5	6-29	18
Dactylopteridae							
Dactylopterus volitans	62	49	13.8	16.5	0.6	11-34	19
Gonostomatidae							
Vinciguerria nimbaria	5,237	38	10.7	1233.9	44.6	27-48	35
Unidentified Gonostomatidae	26	6	1.7	1.9	0.1	32-41	37
Engraulidae							
Anchoviella guineensis	3,098	25	7.0	247.0	8.9	21-34	27
Synodontidae							
Saurida brasiliensis	108	8	2.2	11.0	0.4	14-32	25
Unidentified Synodontidae	106	17	4.8	11.9	0.4	23-39	31
Bothidae							
Unidentified Bothidae	43	23	6.5	5.0	0.2	16-30	23
Balistidae							
Unidentified Balistidae	22	19	5.3	5.1	0.2	4-20	15
Tetraodontidae							
Unidentified Tetraodontidae	22	18	5.1	3.5	0.1	10-18	13
Paralepididae							
Unidentified Paralepididae	64	13	3.7	5.9	0.2	34-71	46
Anguilloidei							
Unidentified Anguilloidei	20	13	3.7	2.7	0.1		
Holocentridae							
Unidentified Holocentridae	12	12	3.4	3.2	0.1	10-36	24
Scorpaenidae							
Unidentified Scorpaenidae	13	12	3.4	1.7	0.1	4-20	13
Blennidae							
Ophioblennius webbi	10	9	2.5	3.3	0.1	29-42	34
Aulopidae							
Aulopus spp.	5	4	1.1	1.4	<0.1	26-45	33

APPENDIX TABLE 1.—Continued.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Bramidae							
Pterycombus brama	2	2	0.6	1.4	<0.1	28-36	32
Taractichthys longipinnis	1	1	0.3	0.3	<0.1		
Unidentified Bramidae	1	1	0.3	0.2	<0.1		
Chiasmodontidae							
Dysalotus spp.	4	4	1.1	2.0	<0.1	18-39	32
Ophichthidae							
Unidentified Ophichthidae	2	2	0.6	0.2	<0.1		
Sternoptychidae							
Sternoptyx diaphana	2	2	0.6	1.4	<0.1	20-26	23
Myctophidae							
Unidentified Myctophidae	10	2	0.6	0.3	<0.1	7-9	8
Chaunacidae							
Chaunax pictus	2	2	0.6	0.2	<0.1	8-9	9
Brotulidae							
Unidentified Brotulidae	2	2	0.6	0.7	<0.1	28-44	36
Exocoetidae							
Unidentified Exocoetidae	2	2	0.6	2.7	<0.1		
Trachipteridae							
Trachipterus trachypterus	2	2	0.6	0.5	<0.1	47-51	49
Triglidae							
Chelidonichthys gabonensis	2	2	0.6	0.6	<0.1	20-22	21
Sphyraenidae							
Sphyraena spp.	3	2	0.6	0.5	<0.1	28-31	29
Uranoscopidae							
Uranoscopus spp.	2	2	0.6	0.5	<0.1	17	17
Trichiuridae							
Unidentified Trichiuridae	4	2	0.6	0.8	<0.1	42-83	68
Istiophoridae							
Unidentified Istiophoridae	2	2	0.6	0.2	<0.1	13-17	15
Monacanthidae							
Unidentified Monacanthidae	2	2	0.6	3.6	0.1	15-51	33
Ostraciontidae							
Unidentified Ostraciontidae	2	2	0.6	0.3	<0.1	8-10	9
Congridae							
Unidentified Congridae	1	1	0.3	0.2	<0.1		
Antennariidae							
Unidentified Antennariidae	1	1	0.3	0.3	<0.1		
Aulostomidae							
Aulostomus maculatus	1	1	0.3	0.2	<0.1		
Stromatedoidei							
Unidentified Stromatedoidei	1	1	0.3	0.1	<0.1		
Ariommidae							
Ariomma spp.	1	1	0.3	1.3	<0.1		
Chaetodontidae							
Unidentified Chaetodontidae	1	1	0.3	0.2	<0.1		
Crustaceans:							
Unidentified Crustacea	--	52	14.6	17.0	0.6		
Stomatopoda							
Unidentified Stomatopoda	346	115	32.3	49.8	1.8		
Decapoda							
Brachyura (megalopae)	268	26	7.3	13.3	0.5		
Brachyura (zoea)	7	1	0.3	0.2	<0.1		
Raninidae (megalopae)	473	55	15.4	44.0	1.6		
Grapsidae (megalopae)	2	2	0.6	0.3	<0.1		
Anomoura							
Porcellanidae (megalopae)	9	2	0.6	0.3	<0.1		
Dardanus pectinatus (Glaucothoë)	20	11	3.1	1.9	<0.1		
Petrochirus sp. (Glaucothoë)	4	4	1.1	0.5	<0.1		
Unidentified Paguridea (Glaucothoë)	11	11	3.1	0.4	<0.1		
Macrura-Natantia							
Sergestes sp.	1	1	0.3	0.3	<0.1		
Lucifer sp.	1	1	0.3	0.3	<0.1		

APPENDIX TABLE 1.—Continued.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Caridea							
Brachycarpus biuguinculatus (Retrocaris spinosa—larval stage)	33	23	6.5	2.8	<0.1		
Eretmocaris sp. (larvae of *Lysmata* sp.—Hyppolytidae)	1	1	0.3	0.1	<0.1		
Enoplometopus antilensis	1	1	0.3	0.5	<0.1		
Heterocarpus ensifer	7	6	1.7	1.0	<0.1		
Procletes stage *(Heterocarpus ensifer)*	4	3	0.8	0.4	<0.1		
Anisocaris sp. (larval Caridean genus)	1	1	0.3	0.2	<0.1		
Hippolytidae (larvae)	1	1	0.3	0.1	<0.1		
Unidentified Caridea	14	13	3.7	1.7	<0.1		
Macrura-Reptantia (all Phyllosoma stages)							
Unidentified Macrura-Reptantia	1	2	0.6	0.3	<0.1		
Panulirus rissoni	1	1	0.3	0.2	<0.1		
Amphipoda (Hyperidea)							
Phrosina semilunata	56	42	11.8	9.0	0.3		
Brachyscellus spp.	49	35	9.8	4.4	0.2		
Phronima sedentaria	52	41	11.5	7.9	0.3		
Oxycephalus clausii	10	10	2.8	1.1	<0.1		
Platyscellus ovoides	6	6	1.7	0.8	<0.1		
Anchylomera blossevillei	3	2	0.6	0.2	<0.1		
Vibilia cultripes	1	1	0.3	0.1	<0.1		
Streetsia challengeri	1	1	0.3	0.1	<0.1		
Platyscellus armatus var. *inermis*	1	1	0.3	0.1	<0.1		
Unidentified Hyperidea	9	4	1.1	1.8	<0.1		
Copepoda							
Unidentified Copepoda	6	3	0.8	0.3	<0.1		
Isopoda							
Cymathoidae	1	1	0.3	0.1	<0.1		
Euphausiacea							
Euphausia hanseni	5	5	1.4	0.5	<0.1		
Mollusks:							
Cephalopoda (adults and juveniles)							
Unidentified Cephalopoda	18	15	4.2	9.6	0.3		
Octopoda	27	13	3.7	10.0	0.4		
Argonauta argo	4	1	0.3	9.0	0.3		
Teuthoidea							
Unidentified Ommastrephidae	189	28	7.9	129.1	4.7		
Unidentified Teuthoidea	99	84	23.6	41.8	1.5		
Gastropoda							
Pteropoda							
Cavolinia longirostris	923	17	4.8	20.4	0.7		
Diacria trispinosa	1	1	0.3	0.1	<0.1		
Heteropoda							
Oxygyrus keraudreni	1	1	0.3	0.1	<0.1		
Atlanta peroni	2	2	0.6	0.2	<0.1		
Miscellaneous:							
Salpidae	85	49	13.8	63.0	2.3		
Polychaeta	1	1	0.3	0.2	<0.1		
Syphonophora	1	1	0.3	0.1	<0.1		
Unidentifiable		23	6.5	5.0	0.2		

APPENDIX TABLE 2.—List of forage organisms found in stomachs from 83 yellowfin tunas collected off the west coast of Africa during cruise UN6801. Number of organisms, frequency of occurrence, and percentage of total volume are given for each taxon. Size range and mean sizes are given only for certain forage fishes. Fishes are listed in decreasing order of frequency of occurrence by families; crustaceans, mollusks, and miscellaneous groups are listed by broad categories.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Fishes:							
Unidentifiable	748	69	83.1	230.0	10.4	11-43	27
Carangidae							
Vomer setapinnis	101	36	43.4	23.3	0.9	8-32	16
Decapterus spp.	1	1	1.2	0.8	<0.1		
Naucrates ductor	1	1	1.2	55.0	2.2		
Unidentified Carangidae	107	31	37.3	14.3	0.6	9-40	19
Mullidae							
Pseudopeneus prayensis	386	24	28.9	227.4	9.3	23-51	42
Unidentified Mullidae	315	20	24.1	136.2	5.5	39-51	44
Priacanthidae							
Priacanthus spp.	66	31	37.3	17.3	0.7	13-34	20
Priacanthus arenatus	15	10	12.0	9.1	0.4	18-32	27
Priacanthus cruenatus	1	1	1.2	0.7	<0.1		29
Acanthuridae							
Acanthurus monroviae	50	8	9.6	11.3	0.5	15-27	23
Unidentified Acanthuridae	44	26	31.3	7.7	0.3	11-30	20
Scombridae							
Euthynnus alleteratus	58	21	25.3	18.0	0.7	11-70	33
Auxis spp.	7	5	6.0	1.4	<0.1	12-50	22
Thunnus spp.	3	3	3.6	0.8	<0.1	29-40	36
Katsuwonus pelamis	1	1	1.2	0.2	<0.1		38
Gonostomatidae							
Vinciguerria nimbaria	1,163	23	27.7	518.8	21.1	32-50	40
Unidentified Gonostomatidae	78	7	8.4	24.5	1.0	17-44	29
Bothidae							
Unidentified Bothidae	86	29	34.9	11.2	0.5	15-50	24
Dactylopteridae							
Dactylopterus volitans	45	25	30.1	5.9	0.2	10-25	17
Balistidae							
Unidentified Balistidae	84	23	27.7	16.0	0.7	10-19	14
Gempylidae							
Gempylus serpens	9	6	7.2	2.8	<0.1	44-118	65
Nealotus tripes	2	2	2.4	1.1	<0.1	19-71	45
Nesiarchus nasutus	1	1	1.2	0.2	<0.1		
Promethichthys prometheus	1	1	1.2	0.2	<0.1		
Unidentified Gempylidae	14	12	14.5	3.5	<0.1		
Serranidae							
Unidentified Serranidae	43	18	21.7	7.1	0.3	16-26	21
Lutjanidae							
Unidentified Lutjanidae	29	17	20.5	5.1	0.2	14-38	22
Tetraodontidae							
Unidentified Tetraodontidae	18	16	19.3	3.8	0.2	9-36	16
Blenniidae							
Ophioblennius webbi	27	14	16.9	7.8	0.3	15-40	32
Paralepididae							
Unidentified Paralepididae	130	13	15.7	37.2	1.5	36-100	66
Holocentridae							
Myripristis jacobus	2	2	2.4	0.6	<0.1	22-26	24
Unidentified Holocentridae	20	11	13.3	5.8	0.2	11-32	23
Scorpaenidae							
Unidentified Scorpaenidae	13	13	15.7	3.2	<0.1	11-29	18
Anguilloidei							
Unidentified Anguilloidei	25	11	13.3	2.7	<0.1		
Sternoptychidae							
Sternoptyx diaphana	7	5	6.0	7.0	0.3	25-32	29
Unidentified Sternoptychidae	4	3	3.6	1.9	<0.1	20-27	24
Unidentified Stromateoidei	8	6	7.2	1.8	<0.1	18-34	26
Aulopidae							
Aulopus spp.	11	5	6.0	5.7	0.2	26-49	38

APPENDIX TABLE 2.—Continued.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Trachipteridae							
Trachipterus trachypterus	8	5	6.0	4.0	0.2	45-70	53
Syngnathidae							
Hippocampus spp.	2	1	1.2	0.1	<0.1	16-22	19
Hippocampus punctulatus	2	2	2.4	1.2	<0.1	50-52	51
Unidentified Syngnathidae	2	2	2.4	0.3	<0.1		
Ophichthidae							
Unidentified Ophichthidae	19	4	4.8	2.1	<0.1	80-108	96
Bramidae							
Pterycombus brama	1	1	1.2	0.4	<0.1		
Unidentified Bramidae	2	2	2.4	0.4	<0.1	14-19	17
Nettastomidae							
Unidentified Nettastomidae	7	2	2.4	1.0	<0.1		
Congridae							
Unidentified Congridae	7	2	2.4	2.1	<0.1	80-178	129
Synodontidae							
Saurida brasiliensis	7	1	1.2	1.2	<0.1	31-32	32
Unidentified Synodontidae	1	1	1.2	0.1	<0.1		
Myctophidae							
Unidentified Myctophidae	3	2	2.4	0.3	<0.1	14-23	19
Antennariidae							
Unidentified Antennariidae	3	2	2.4	1.9	<0.1	16-21	18
Monacanthidae							
Unidentified Monacanthidae	2	2	2.4	1.2	<0.1	17-38	28
Ophidiidae							
Ophidion barbatum	23	2	2.4	1.4	<0.1	32-37	35
Fistulariidae							
Fistularia spp.	2	2	2.4	0.3	<0.1	70-86	78
Triglidae							
Unidentified Triglidae	2	2	2.4	0.5	<0.1	21-22	22
Diretmidae							
Diretmus argenteus	1	1	1.2	3.1	0.1		
Nemichthyidae							
Unidentified Nemichthyidae	1	1	1.2	0.1	<0.1		
Brotulidae							
Unidentified Brotulidae	1	1	1.2	0.8	<0.1		
Trachichthyidae							
Gephyroberyx darwini	1	1	1.2	1.0	<0.1		
Grammicolepididae							
Xenolepidichthys spp.	1	1	1.2	0.3	<0.1		
Caproidae							
Antigonia capros	1	1	1.2	3.1	0.1		
Trachipteroidei							
Unidentified Trachipteroidei	1	1	1.2	0.1	<0.1		
Coryphaenidae							
Coryphaena hippurus	1	1	1.2	0.1	<0.1		
Chaetodontidae							
Unidentified Chaetodontidae	1	1	1.2	0.1	<0.1		
Sphyraenidae							
Sphyraena spp.	1	1	1.2	0.2	<0.1		
Chiasmodontidae							
Dysalotus spp.	1	1	1.2	1.0	<0.1		
Istiophoridae							
Unidentified Istiophoridae	1	1	1.2	0.2	<0.1		
Tetragonuridae							
Tetragonurus cuvieri	4	1	1.2	154.0	6.3	165-183	174
Crustaceans:							
Unidentified Crustacea	--	12	14.5	11.2	0.5		
Stomatopoda							
Unidentified Stomatopoda (larvae)	1,081	63	75.9	161.9	6.6		
Decapoda							
Brachyura (megalopae)	287	19	22.9	31.3	1.3		
Unidentified Raninidae (megalopae)	235	23	27.7	25.1	1.0		
Unidentified Grapsidae (megalopae)	8	2	2.4	1.0	<0.1		

APPENDIX TABLE 2.—Continued.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Paguridea (all Glaucothoë)							
Dardanus spp.	3	3	3.6	0.3	<0.1		
Dardanus pectinatus	89	11	13.3	9.5	0.4		
Petrochirus sp.	1	1	1.2	0.1	<0.1		
Unidentified Paguridea	10	4	4.8	1.0	<0.1		
Macrura-Natantia							
Caridea							
Unidentified Pandalidae (larvae)	14	6	7.2	3.9	0.2		
Paciphaeu semispinosa	10	1	1.2	4.0	0.2		
Heterocarpus ensifer	1	1	1.2	0.2	<0.1		
Procletes stage (*Heterocarpus ensifer*)	6	3	3.6	0.9	<0.1		
Anisocaris sp. (larval genus)	5	2	2.4	0.5	<0.1		
Eretmocaris sp. (larval genus)	2	2	2.4	0.3	<0.1		
Oplophorus sp. (larval genus)	1	1	1.2	0.1	<0.1		
Enoplometopus antilensis	6	5	6.0	2.0	<0.1		
Unidentified Caridea	16	9	10.8	4.6	0.2		
Macrura-Reptantia (all Phyllosoma stages)							
Scyllarus arctus	5	2	2.4	1.2	<0.1		
Unidentified Macrura-Reptantia	6	3	3.6	0.6	<0.1		
Amphipoda (Hyperiidea)							
Phrosina semilunata	73	29	34.9	14.6	0.6		
Brachyscellus sp.	58	14	16.9	4.8	0.2		
Phronima sedentaria	17	8	9.6	2.0	<0.1		
Oxycephalus clausii	9	6	7.2	0.9	<0.1		
Platyscellus ovoides	1	1	1.2	0.1	<0.1		
Streetsia challengeri	1	1	1.2	0.1	<0.1		
Euphausiacea							
Euphausia hanseni	26	6	7.2	1.3	<0.1		
Mollusks:							
Cephalopoda (adults and juveniles)							
Unidentified Cephalopoda	48	12	14.5	30.7	1.2		
Octopoda							
Argonauta sp.	1	1	1.2	1.5	0.1		
Tremoctopus violaceus	9	1	1.2	4.5	0.2		
Octopus sp.	5	2	2.4	2.8	<0.1		
Unidentified Octopoda	25	12	14.5	31.6	1.3		
Teuthoidea							
Unidentified Ommastrephidae	437	36	43.4	314.2	12.8		
Unidentified Chiroteuthidae	1	1	1.2	1.0	<0.1		
Ornithoteuthis antilarum	5	1	1.2	1.5	<0.1		
Liocranchia reinhardti	11	1	1.2	5.0	0.2		
Liocranchia sp.	1	1	1.2	0.2	<0.1		
Cranchia scabra	3	2	2.4	3.2	0.1		
Onychoteuthis banksi	1	1	1.2	0.4	<0.1		
Mastigoteuthis sp.	1	1	1.2	0.5	<0.1		
Onykia sp.	4	2	2.4	5.5	0.2		
Unidentified Cranchiidae	5	3	3.6	2.8	0.1		
Unidentified Enoploteuthidae	4	3	3.6	1.7	<0.1		
Unidentified Teuthoidea	204	45	54.2	124.6	5.1		
Gastropoda							
Unidentified Atlantidae	2	2	2.4	0.2	<0.1		
Miscellaneous:							
Salpidae	27	17	20.5	8.8	0.4		

APPENDIX TABLE 3.—List of forage organisms fond in stomachs from 202 skipjack tunas, collected off the west coast of Africa during cruise UN6802. Number of organisms, frequency of occurrence, and percentage of total volume are given for each taxon. Size ranges and mean sizes are given only for certain forage fishes. Fishes are listed in decreasing order of frequency of occurrence by families; crustaceans, mollusks, and miscellaneous groups are listed by broad categories.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Fishes:							
Unidentifiable	698	155	76.7	109.3	11.1		
Paralepididae							
Unidentifiable Paralepididae	1,026	59	29.2	280.5	28.4	52-112	68
Carangidae							
Vomer setapinnis	44	33	16.3	24.0	2.4	9-36	27
Trachinotus ovatus	4	4	2.0	0.6	0.1	17-23	19
Unidentified Carangidae	15	13	6.4	6.0	0.6	11-56	22
Gempylidae							
Gempylus serpens	1	1	0.5	0.3	0.1		
Unidentified Gempylidae	25	17	8.4	11.9	1.2	62-94	78
Trichiuridae							
Unidentified Trichiuridae	49	18	8.9	13.6	1.4	66-110	94
Scombridae							
Auxis spp.	33	10	5.0	8.6	0.9	15-63	31
Sarda sarda	4	4	2.0	2.3	0.2	25-43	34
Scomber japonicus	1	1	0.5	1.3	0.1		
Serranidae							
Unidentified Serranidae	152	12	5.9	15.0	1.5	14-25	19
Scorpaenidae							
Unidentified Scorpaenidae	13	10	5.0	2.6	0.3	15-25	18
Lutjanidae							
Unidentified Lutjanidae	9	7	3.5	1.4	0.1	15-24	19
Berycoidei							
Unidentified Berycoidei	8	8	4.0	1.4	0.1	13-17	15
Percoidei							
Unidentified Percoidei	257	6	3.0	85.1	8.6	19-32	27
Anguilloidei							
Unidentified Leptocephalus	6	5	2.5	0.7	0.1		
Bothidae							
Unidentified Bothidae	7	5	2.5	1.1	0.1	20-30	25
Acanthuridae							
Unidentified Acanthuridae	4	4	2.0	0.8	0.1	13-17	15
Trachipteridae							
Trachipterus trachypterus	4	4	2.0	2.6	0.3		
Triglidae							
Unidentified Triglidae	5	5	2.5	1.2	0.1	17-23	20
Chaetodontidae							
Chaetodon spp.	4	3	1.5	2.3	0.2	12-35	23
Clupeoidei							
Unidentified Clupeoidei	70	3	1.5	4.7	0.5		
Syngnathidae							
Unidentified Syngnathidae	2	2	1.0	0.7	0.1	100-113	106
Synodontidae							
Unidentified Synodontidae	14	2	1.0	2.0	0.2		
Alepisauridae							
Alepisaurus ferox	1	1	0.5	3.6	0.4		
Holocentridae							
Unidentified Holocentridae	1	1	0.5	0.5	0.1		
Ophidiidae							
Unidentified Ophidiidae	2	2	1.0	1.4	0.1		
Priacanthidae							
Priacanthus spp.	1	1	0.5	0.2	<0.1		
Stromateoidei							
Unidentified Stromateoidei	2	1	0.5	2.5	0.2	23-53	38
Tetraodontidae							
Unidentified Tetraodontidae	1	1	0.5	0.1	<0.1		
Uranoscopidae							
Uranoscopus spp.	1	1	0.5	0.8	0.1		

APPENDIX TABLE 3.—Continued.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Crustaceans:							
Amphipoda (Hyperiidea)							
Phrosina semilunata	561	139	68.8	83.8	6.2		
Brachyscellus spp.	281	94	46.5	18.9	1.4		
Phronima sedentaria	39	26	12.9	4.3	0.3		
Anchylomera blossevillei	27	3	1.5	1.2	<0.1		
Platyscellous ovoides	9	6	3.0	0.7	<0.1		
Vibilia armata	6	6	3.0	0.6	<0.1		
Platyscellus serratulus	2	2	1.0	0.4	<0.1		
Platyscellus armatus inermis	1	1	0.5	0.2	<0.1		
Oxycephalus clausi	1	1	0.5	0.1	<0.1		
Decapoda							
Raninidae (megalopae)	112	58	28.7	9.0	0.7		
Brachyura (megalopae)	16	13	6.4	1.9	0.1		
Stomatopoda (larval forms)	43	31	15.3	5.4	0.4		
Euphausiacea							
Euphausia hanseni	3,556	19	9.4	118.0	8.8		
Anomura							
Paguridea (all Glaucothoë)							
Dardanus pectinatus	9	7	3.5	0.9	<0.1		
Macrura-Reptantia (all Phyllosomae larvae)							
Scyllarus arctus	5	5	2.5	0.9	<0.1		
Scyllarus sp.	2	2	1.0	0.2	<0.1		
Scyllarides sp.	1	1	0.5	0.1	<0.1		
Macrura-Natantia							
Sergestidae	1	1	0.5	0.2	<0.1		
Lucifer sp.	1	1	0.5	0.1	<0.1		
Caridea	1	1	0.5	0.1	<0.1		
Palaemonidae	1	1	0.5	0.1	<0.1		
Copepoda							
Arietellus armatus	1	1	0.5	0.1	<0.1		
Candacia varicans	1	1	0.5	0.1	<0.1		
Unidentifiable Crustacea				0.9	<0.1		
Mollusks:							
Cephalopoda (adults and juveniles)							
Unidentified Cephalopoda	14	13	6.4	3.2	0.2		
Octopoda							
Argonauta sp.	2	2	1.0	6.7	0.5		
Other Octopoda	1	1	0.5	0.1	<0.1		
Teuthoidea							
Ornithoteuthis antillarum	78	33	16.3	126.4	10.1		
Ommastrephidae	37	31	15.3	9.4	0.7		
Unidentified Teuthoidea	4	3	1.5	0.3	<0.1		
Gastropoda							
Pteropoda							
Cavolinia longirostris	39	12	5.9	1.8	<0.1		
Heteropoda							
Atlantidae	4	4	2.0	0.3	<0.1		
Atlanta sp.	2	2	1.0	0.2	<0.1		
Atlanta peroni	1	1	0.5	0.1	<0.1		
Oxygyrus keraudreni	1	1	0.5	0.1	<0.1		
Miscellaneous:							
Salpidae	8	7	3.5	1.1	<0.1		

APPENDIX TABLE 4.—List of forage organisms found in stomachs from 43 yellowfin tunas, collected off the west coast of Africa during cruise UN6802. Number of organisms, frequency of occurrence, and percentage of total volume are given for each taxon. Size ranges and mean sizes are given only for certain forage fishes. Fishes listed in decreasing order of frequency of occurrence; crustaceans, mollusks, and miscellaneous groups are listed by broad categories.

Taxon	Number of organisms	Frequency of occurrence		Volume		Size (mm)	
		Number	%	ml	%	Range	Mean
Fishes:							
Unidentifiable	238	38	88.4	61.1	17.1		
Scombridae							
Auxis spp.	53	11	25.6	7.4	2.1	15-34	22
Sarda sarda	4	2	4.7	0.5	0.1	15-21	18
Scomber japonicus	1	1	2.3	0.1	<0.1		
Unidentified Scombridae	15	6	14.0	0.8	0.2		
Carangidae							
Vomer setapinnis	14	10	23.3	4.5	1.2		
Unidentified Carangidae	3	3	7.0	5.3	1.5	21-98	48
Paralepididae							
Unidentified Paralepididae	10	5	11.6	2.1	0.6		
Gempylidae							
Gempylus serpens	3	3	7.0	0.4	0.1		
Unidentified Gempylidae	2	1	2.3	0.1	<0.1		
Trichiuridae							
Unidentified Trichiuridae	4	3	7.0	2.1	0.6		
Chaetodontidae							
Chaetodon spp.	2	2	4.7	2.5	0.7	20-35	27
Exocoetidae							
Cypselurus spp.	1	1	2.3	27.5	7.7		
Unidentified Exocoetidae	1	1	2.3	7.0	1.9		
Percoidei							
Unidentified Percoidei	16	2	4.7	5.0	1.4	20-28	24
Trachipteridae							
Trachipterus trachypterus	3	2	4.7	9.2	2.6		
Alepisauridae							
Alepisaurus ferox	1	1	2.3	20.0	5.6		
Bothidae							
Unidentified Bothidae	1	1	2.3	0.1	<0.1		
Ophidiidae							
Unidentified Ophidiidae	1	1	2.3	2.0	0.6		
Syngnathidae							
Unidentified Syngnathidae	1	1	2.3	0.3	0.1		
Crustaceans:							
Stomatapoda (larval forms)	81	24	55.8	7.4	2.1		
Amphipoda (Hyperiidea)							
Phrosina semilunata	62	19	44.2	9.4	2.6		
Brachyscelus spp.	8	6	13.9	0.7	1.9		
Phronima sedentaria	8	4	9.3	1.3	3.6		
Vibilia armata	1	1	2.3	0.1	0.1		
Decapoda							
Brachyura (megalopae)	13	4	9.3	1.7	0.5		
Raninidae (megalopae)	5	4	9.3	0.4	0.1		
Anomura							
Macrura-Reptantia (all phyllosemae larvae)							
Scyllaridae sp.	2	2	4.6	0.2	0.1		
Scyllarus sp.	2	2	4.6	0.2	<0.1		
Paguridea (all Glaucothoë)							
Dardanus pectinatus	4	2	4.6	0.4	1.1		
Unidentifiable Crustacea				0.4	1.1		
Mollusks:							
Cephalopoda (adults and juveniles)							
Unidentified Cephalopoda	7	6	13.9	3.5	1.0		
Octopoda							
Argonauta argo	6	5	11.6	165.5	46.3		
Teuthoidea							
Ommastrephidae	10	2	4.6	4.6	1.3		
Ornitheteuthis antillarum	2	2	4.6	1.3	0.4		
Tetrenychoteuthis dusumieri	1	1	2.3	1.3	0.4		
Unidentified Teuthoidea	4	4	9.2	0.4	1.1		
Miscellaneous:							
Salpidae	4	3	6.9	0.3	0.1		

FOOD HABITS OF JUVENILE MARINE FISHES: EVIDENCE OF THE CLEANING HABIT IN THE LEATHERJACKET, *OLIGOPLITES SAURUS*, AND THE SPOTTAIL PINFISH, *DIPLODUS HOLBROOKI*

WILLIAM E. S. CARR AND CLAYTON A. ADAMS[1]

ABSTRACT

Quantitative gravimetric analyses of stomach contents of juvenile leatherjacket, *Oligoplites saurus*, and spottail pinfish, *Diplodus holbrooki*, have revealed that both species pass through a stage in which they clean ectoparasites from other fishes. This cleaning stage is most evident in juveniles between 26 and 40 mm standard length and is far less evident among juveniles of larger or smaller size. These findings represent the first report that cleaning is practiced by either species and the first quantitative data on the significance of the cleaning habit to members of the Family Carangidae and Family Sparidae. Neither *O. saurus* nor *D. holbrooki* depend exclusively on cleaning as a source of food. Juveniles of *O. saurus* feed heavily on plankton and small shrimp whereas juveniles of *D. holbrooki* feed heavily on epiphytic algae, plankton, and encrusting organisms. Juveniles of both species exhibit distinct changes in diet during growth.

The important role of the estuarine zone in providing nursery areas utilized by the juvenile stages of a large number of marine fishes is now well documented (Sykes and Finucane, 1966; Smith, Swartz, and Massmann, 1966; and others). Although much is known about the food habits of the adults and subadults of most estuarine-dependent species, only a limited literature exists on the food habits of the smaller juvenile individuals. Consequently, we have been studying the food habits of juveniles of all available species of fishes which inhabit certain nursery areas in the nearshore estuarine zone between the Crystal River and the Withlacoochee River on the northwest coast of Florida. To date our study involves 18 species which we are studying concurrently.

In the course of the investigation described above, we have discovered that juveniles of two species, the leatherjacket, *Oligoplites saurus* (Bloch and Schneider) (a carangid), and the spottail pinfish, *Diplodus holbrooki* (Bean) (a sparid), clean ectoparasites from other fishes. This phenomenon has not been reported previously for either species. The report which follows describes the diets of juveniles of both species and shows that these diets include considerable amounts of ectoparasites and other material obtained by cleaning.

MATERIALS AND METHODS

DESCRIPTION OF STUDY AREA AND SAMPLING METHODS

Specimens of juvenile *Oligoplites saurus* and *Diplodus holbrooki* were collected in the vicinity of the Florida Power Corporation steam electric station located 7.5 miles northwest of the town of Crystal River, Fla. (lat 23°57′N, long 82°45′W). This station is situated approximately 3 miles northwest of the mouth of the Crystal River and 4 miles southeast of the mouth of the Withlacoochee River on the northwest coast of Florida. Sampling sites in this estuarine area were located to the north and south of the dikes delimiting the intake canal of the electric station. The sampling sites were densely vegetated with seagrasses, primarily *Ruppia maritima* and *Diplanthera wrightii*, and several

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types of algae among which two species of *Caulerpa, C. prolifera* and *C. paspaloides,* were most conspicuous. Collections of fishes were made near low tide at which time the depth at the sampling sites was 3 to 4 ft. Specimens analyzed for this report were collected from April 3 to August 25, 1971. Water temperatures at the sampling sites during this period ranged from 17.3° to 33.1°C whereas salinities ranged from 16.4 to 24.1 ‰. All sampling sites were greater than a mile from the zone of influence of thermal discharge from the electric station.

The majority of juvenile fishes used in this study were collected with a bag seine (50 ft × 6 ft) constructed of ⅜-inch stretched mesh netting. A few specimens were collected in a 5-ft cast net constructed of ½-inch stretched mesh netting. Specimens were preserved immediately in 20% Formalin-seawater. In the laboratory, fish were washed in tap water, sorted to species, and stored in 75% isopropyl alcohol. High concentrations of preservative were used to assure adequate preservation of stomach contents. Specimens of adult *D. holbrooki* were collected with hook and line, injected immediately with Formalin, and treated as above.

ANALYSIS OF STOMACH CONTENTS

Juvenile fishes were measured to the nearest 1.0 mm standard length and sorted into size classes of 5-, 10-, or 20-mm increments depending on the number of fish available. All references to fish length are in terms of standard length. After removal of stomachs, food items were removed in alcohol with the aid of a dissecting microscope. Stomach contents from similar size classes were pooled and analyzed as to percent composition using a modified gravimetric procedure which employed a preliminary fractionation of food items with a series of sieves. This procedure is outlined below:

1. Large food items of similar types easily recognizable to the naked eye were removed onto preweighed filter pads (Whatman[2] No. 42, 2.5-inch diameter). This initial step was used only for certain food items (i.e., shrimp, crabs, larval fish, etc.) obtained from fish in the larger size classes.
2. The remaining stomach contents were poured into a series of 3-inch diameter sieves (U.S. Standard Nos. 10, 20, 30, 60, 120, 200) arranged and clamped together in order of decreasing mesh size. Sieves Nos. 10 and 20 were frequently not needed for fractionations of material from fish in very small size classes.
3. The series of sieves was secured to a Burrell "Wrist Action" shaker and shaken gently for 10 to 15 min while washing continuously under slowly flowing water.
4. The contents of each sieve (comprising a sieve fraction) was washed into a finger bowl for detailed analysis beneath a dissecting microscope. Analysis involved adding five large drops of the sieve fraction to a gridded petri dish (13 squares per inch) and recording the frequency of occurrence of each type of food item in each drop. The accuracy of this method is good because all food items in a particular sieve fraction are of comparable size. The portion of the contents of each sieve fraction attributable to each type of food item was recorded.
5. After analysis of all sieve fractions, each fraction was vacuum-filtered onto a separate preweighed filter pad using a Millipore filter holder and a vacuum flask.
6. Filter pads were dried overnight in a drying oven (ca. 70°C) and dry weights of food items were calculated after weighing the pads to the nearest 0.0001 g on a microbalance.

Further comments on the efficacy of this procedure for analyzing the stomach contents of small fish are given in the following section on Results.

RESULTS

OLIGOPLITES SAURUS

Figure 1 shows the results of analyses of stomach contents of juvenile *O. saurus* belonging

[2] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

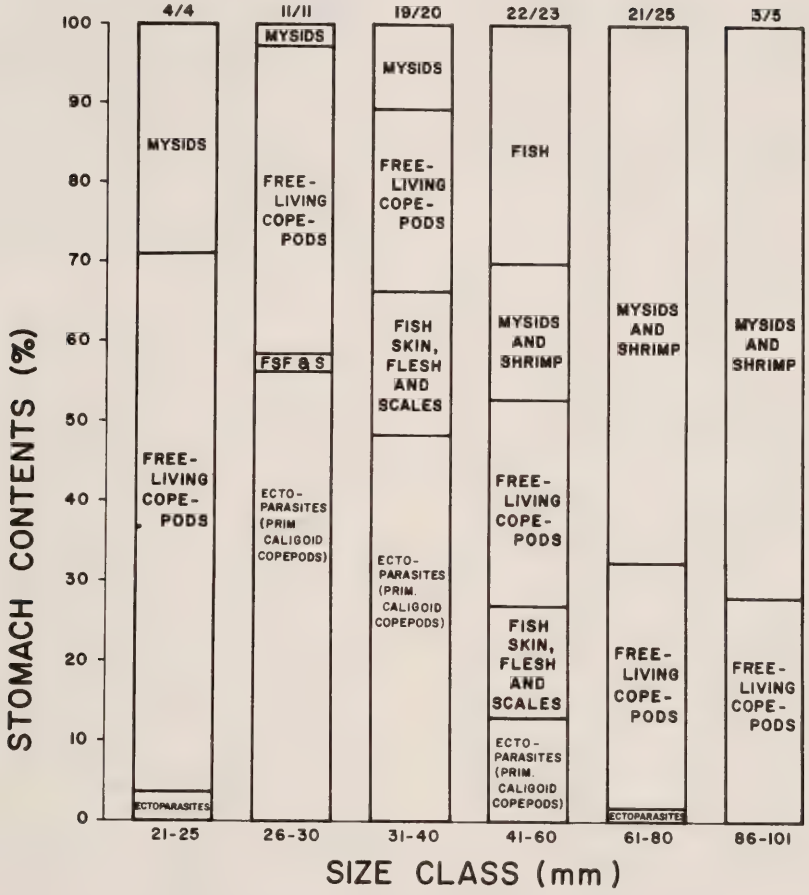

FIGURE 1.—Stomach contents of juveniles of *Oligoplites saurus*. Bar graph for each size class shows percent of total stomach contents attributable to individual food items. Designation of sample size above each bar graph shows fraction of stomachs analyzed which contained food.

to the six size classes obtained in our collections. Juveniles of this species go through a stage in which ectoparasites of fish make a major contribution to their diet. The relative contribution of ectoparasites to the diet is at a maximum in fish that are betweeen 26 and 40 mm long. Ectoparasites account for approximately 56% of the stomach contents of fish 26 to 30 mm long and approximately 48% of the contents of fish 31 to 40 mm long. The majority of the ectoparasites consumed were caligoid copepods; a few were branchiurans, *Argulus* sp. In contrast, ectoparasites constituted only 2 to 4% of the stomach contents in fish less than 26 mm long or greater than 60 mm long. Ectoparasites made up less than 1% of the stomach contents of fish 86 to 100 mm long.

The importance of food material obtained by cleaning in juveniles of this species is even greater if the contribution of bits of fish skin, flesh, and scales is combined with that of ectoparasites (see Figure 1). In leatherjackets between 26 and 60 mm in length, the total portion of the stomach contents attributable to material

obtained from cleaning ranges from 27 to 67% with maximum percentages obtained in 26 to 40 mm fish (58 to 67%).

Most of the fish skin, flesh, and scales present in the stomachs are construed to have come from cleaning activities, since other than occasional fish larvae, fish per se were seldom encountered in any of the stomachs examined.

A sizable portion of the diet of juveniles of all size classes consists of free-living organisms, primarily copepods, mysids, and small shrimp (see Figure 1). Free-living organisms account for 96 to 100% of the stomach contents of juveniles outside the 26 to 60 mm size classes. Free-living copepods comprise the major food item of 21 to 25 mm individuals whereas mysids and small shrimp made up the major food items of fish in the 61 to 100 mm size classes.

Since there were no prior reports on *O. saurus* functioning as a cleaner, additional analyses were made of other specimens collected from other sites at other times. Collections of juvenile *O. saurus* were obtained from Dr. Carter R. Gilbert of the Florida State Museum for this purpose. The results of analyses of these collections are given in Table 1. Ectoparasites were present in the stomachs of fish belonging to all size classes examined. The relative contribution of ectoparasites to the diet was again maximum in fish between 26 and 40 mm in length. A maximum of 24 ectoparasites was recovered from each of two stomachs of fish 41 to 60 mm long. The relative contribution of ectoparasites to the total diet decreased dramatically in fish greater than 60 mm in length. The data from analyses of museum collections correlated remarkably well with the data presented earlier on freshly collected specimens. The lower percentages of stomach contents attributable to ectoparasites in the museum collections may have been due to the fact that these fish had been stored for 10 to 20 years and were not as well preserved as our freshly collected specimens. This was suggested by the presence of significant amounts of unidentifiable debris in the stomachs of the museum fish.

DIPLODUS HOLBROOKI

Figure 2 shows the results of analyses of stomach contents of juvenile *D. holbrooki* in the 10 size classes obtained in our collections. As was the case with *O. saurus*, *D. holbrooki* goes through a juvenile stage in which it is a cleaner. One or more species of the ectoparasitic branchiuran, *Argulus*, is significant in the diet of juveniles between 21 and 50 mm in length. The percentage of ectoparasites in the total stomach contents is maximum in fish 31 to 35 mm long (20%) with somewhat smaller percentages recorded in fish 26 to 30 mm long and in fish 36 to 40 mm long. A maximum of 16 ectoparasites (*Argulus*) was recovered from the stomach of a single fish in the 36 to 40 mm size class. The relative contribution of ectoparasites to the total stomach contents decreases dramatically to less than 1% in fish less than 61 mm long. Only one ectoparasite was found in the stomachs of 35 fish 61 to 70 mm long. Ectoparasites were absent from the stomachs of fish less than 21 mm or greater than 70 mm in length. Likewise, ectoparasites were absent from the stomachs of 18

TABLE 1.—Analyses of stomach contents of *Oligoplites saurus* obtained from Florida State Museum.[1]

Size class (mm)	Number of fish	Number of stomachs with food	Stomachs with food and ectoparasites		Number of ectoparasites per stomach with food		Ectoparasites - % of total stomach contents
			Number	Percent	Average	Range	
21-25	2	1	1	100	2	(2)	Not determined
26-30	5	5	4	80	1.4	(0-3)	26
31-40	12	11	9	82	4.1	(0-9)	21
41-60	23	21	19	90	6.8	(0-24)	13
61-80	15	15	13	87	3.1	(0-12)	3
81-100	7	7	3	43	0.4	(0-1)	0.3

[1] Fish taken from collections indicated as follows:
Cedar Key, Fla., 10/27/47, 7/24/48, 10/24/48, 9/25/53.
Little Gasparilla Pass, Charlotte Co., Fla., 7/21/60.

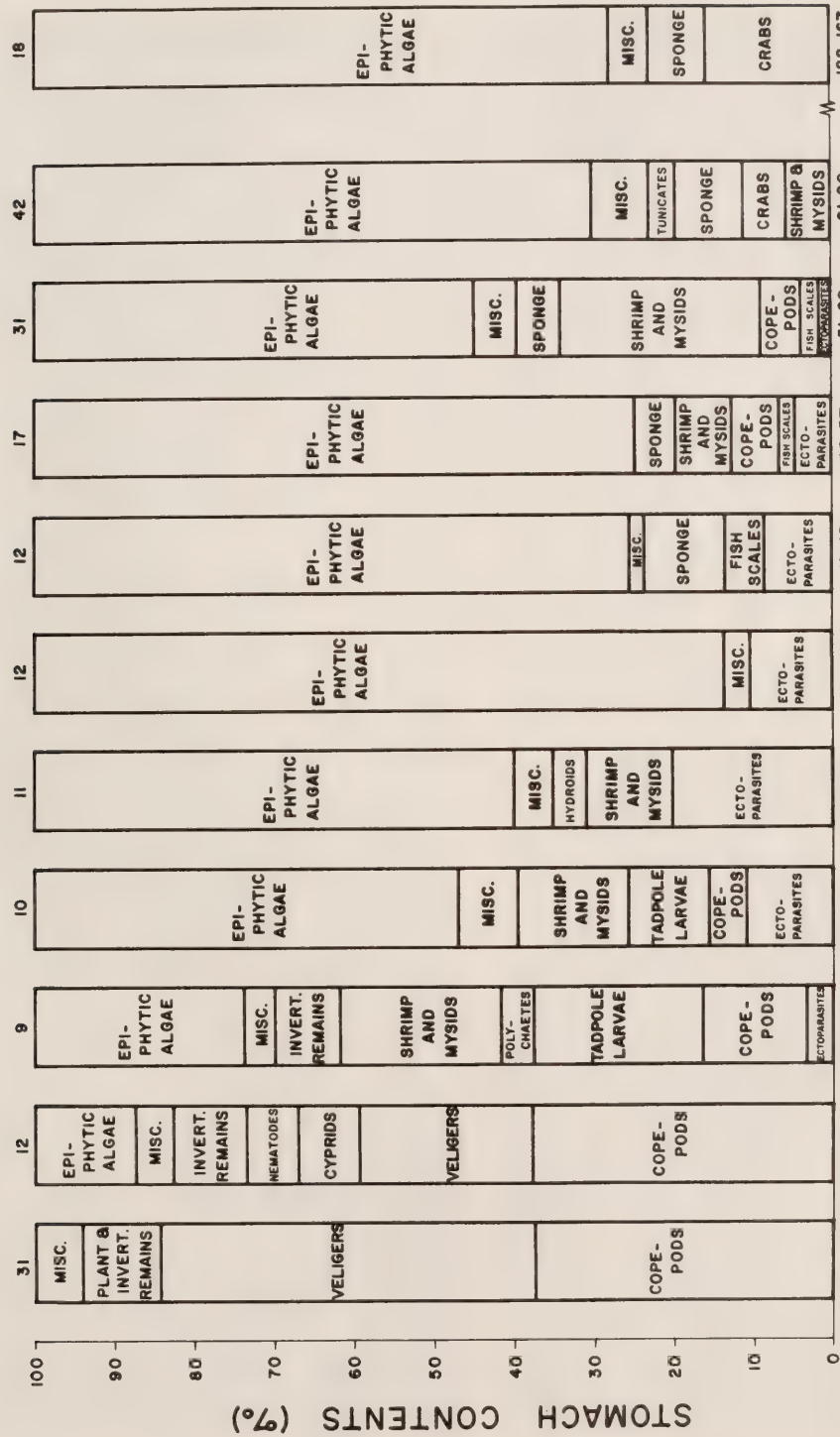

FIGURE 2.—Stomach contents of juveniles of *Diplodus holbrooki*. Presentation same as in Figure 1. Sample size above each bar graph shows number of stomachs with food which were analyzed. Misc. = combination of all items which individually account for less than 3% of total.

adult *Diplodus* which were analyzed. Fish scales were a common constituent of stomachs of fish in size classes between 21 and 70 mm in length. The contribution of fish scales to the stomach contents was at a maximum in 41 to 45 mm fish (5%). The majority of the fish scales present in stomachs are construed to have come from cleaning activities since fish per se were seldom encountered in the stomachs of any of the *Diplodus* examined.

As shown in Figure 2, the bulk of the diet of juvenile *D. holbrooki* consists of free-living animals and epiphytic algae. Cleaning activities provide only a modest portion of the total food ingested by fish in any of the size classes. Individuals in size classes between 11 and 25 mm are primarily planktivorous with veligers, copepods, tunicate tadpole larvae, mysids, and small shrimp accounting for 56 to 87% of the total stomach contents. Fish over 25 mm become very dependent on plant material in the form of epiphytic algae. This plant material accounts for 53 to 87% of the total stomach contents of all size classes above 26 mm in length, including adults. However, variable amounts of animal material, especially sponge, copepods, shrimp, and mysids, are also consumed. Stomach contents of fish greater than 25 mm in length show that *Diplodus* feeds heavily on plant and animal material which grows attached to other subjects. Even the crabs consumed by larger individuals are primarily porcellanids (*Petrolisthes* sp.) that live in association with submerged rock and shell.

Since there are no prior reports of *D. holbrooki* functioning as a cleaner, additional juvenile specimens were obtained from Dr. Carter R. Gilbert. These specimens were collected in 1951 and 1957 near Cedar Key, Fla. Unfortunately, the museum collections were short on specimens in the 21 to 60 mm size range and those that were provided did not have well-preserved stomach contents. All that can be stated with certainty from these specimens is that ectoparasites did appear in stomachs of 5 of the 13 fish available in the size range of 26-35 mm. Representatives of other juvenile size classes were either not available or inadequately preserved for analysis.

EFFICACY OF SIEVE FRACTIONATION PROCEDURE

The sieve fractionation procedure described in Materials and Methods has contributed greatly to our capacity to analyze quantitatively the stomach contents of very small fish. This procedure provides a convenient means of separating a heterogeneous mixture of minute food items into fractions which are individually quite homogeneous with respect to particle size. Table 2 presents the format used and the results obtained following a sieve fractionation of stomach contents of *D. holbrooki* belonging to the 11 to 15 mm size class. This table and the following discussion are provided to illustrate the efficacy of this procedure. After identification of the food items in each sieve fraction (Column A), the determination of the portion of each fraction attributable to a particular food item (Column B) is eased considerably by the fact that all items in the fraction are of comparable size. After determining the dry weight of each fraction (Column C), the contribution of individual food items (Column D) is estimated by multiplying the weight of the fraction by the value defining the portion of the fraction attributable to that food item. Finally, the total amounts and percentages of the entire stomach contents which are attributable to the individual food items are determined by simple compilation (Columns E and F). This procedure has now been employed in this laboratory to analyze the stomach contents of juvenile stages of 18 species of fishes.

DISCUSSION

Randall (1967) has described the Carangidae as a family of carnivorous fish whose food habits may be divided into three major categories: fish feeders, plankton feeders, and mollusk feeders. His classification was based primarily on feeding habits of adult fish, and it was recognized that not all of the species, including their juvenile stages, fit perfectly into these categories. Randall analyzed stomach contents of *Oligoplites saurus* (149 to 234 mm) from the West Indies and found this carangid to be primarily a fish feeder. Similar findings have been reported by

TABLE 2.—Data obtained from sieve fractionation and gravimetric analysis of stomach contents of 31 juvenile *D. holbrooki* in 11-15 mm size class.

Sieve mesh size[1]	(Col. A) Food item	(Col. B) Portion of Sieve fraction attributable to food item	(Col. C) Dry weight of entire sieve fraction (mg)	(Col. D) Calculated weight of food item (mg)
No. 60-250 μ	Copepods	0.47	3.5	1.6
	Veligers	0.38		1.3
	Cyprids	0.07		0.3
	Nematodes	0.07		0.3
No. 120-125 μ	Copepods	0.40	3.2	1.3
	Veligers	0.60		2.0
	Nematodes	<0.01		<0.1
No. 200-74 μ	Copepods (larval)	0.17	2.2	0.4
	Veligers	0.43		0.9
	Animal remains	0.22		0.5
	Plant remains	0.17		0.4

Summarization of data:

Food item	(Col. E) Total dry weight (mg)	(Col. F) Percent of total sample
Copepods	3.3	37
Veligers	4.2	47
Cyprids	0.3	3
Nematodes	0.3	3
Animal remains	0.5	6
Plant remains	0.4	4
Total	9.0	100

[1] A No. 30 sieve (595 μ) also used in sieve series employed here, but it retained none of the items consumed by 11- to 15-mm fish.

Beebe and Tee-Van (1928) on specimens from Haiti and by Springer and Woodburn (1960) on specimens from Tampa Bay, Fla. Tabb and Manning (1961) reported that this species (30 to 120 mm) in Florida Bay feeds heavily on snapping shrimp and small pink shrimp in addition to fish larvae. With the exception of the modest data presented by Randall (1967), the literature is devoid of quantitative information on the food habits of this common inshore species. No prior reports have been made on this species acting as a cleaner.

Our quantitative determinations of the stomach contents of juvenile *O. saurus* (21 to 80 mm) collected near Crystal River, Fla., show clearly that this carangid passes through a stage in the initial year of its development in which intensive cleaning behavior is implicated. Food materials obtained from cleaning activities, especially caligoid copepods, account for 58 to 67% of the stomach contents of fish 26 to 40 mm in length (see Figure 1). Lesser amounts of such material were present in fish outside of this size range. Although no observations were made of *Oligoplites* actually engaged in cleaning activities in the field, it is extremely unlikely that any other type of feeding activity can account for these results. If ectoparasites, such as caligoid copepods, were readily ingested from the plankton, then they would be expected to be common in the stomachs of the planktivorous stages of other species of fishes in the area. We have analyzed the stomachs of more than 6,000 juvenile fishes belonging to 18 species present in our study area and, aside from a single *Argulus* sp. found in the stomachs of one *Orthopristes chrysopterus* and one *Menidia beryllina*, have found no ectoparasites or other indicators of cleaning activity in species other than *O. saurus* and *D. holbrooki*. The only other reports of cleaning behavior among the carangids are brief accounts given by divers on the pilotfish (*Naucrates ductor*) and young bar jack (*Caranx ruber*) (Hass, 1953; Randall, 1962).

Although many studies have been done on various aspects of the biology of members of the Family Sparidae, the literature contains only one very brief account of an apparent cleaning

episode involving a member of this family. Breder (1962) noted a single juvenile *Lagodon rhomboides* picking at the pelvic axils of three successive *Mugil cephalus* in Lemon Bay, Fla. Breder commented that this was the only time he had observed this interaction although he was thoroughly familiar with both species.

Our analyses of stomach contents of juvenile *D. holbrooki* (11 to 80 mm, see Figure 2) show clearly that this species, like *O. saurus*, goes through a stage in the initial year of its development in which cleaning behavior is implicated. Concurrent analyses of more than 3,000 stomachs of juveniles of another sparid, *Lagodon rhomboides* (10 to 130 mm), collected from the same area failed to yield a single ectoparasite or other evidence of cleaning activity in this related species. Data on food habits of *L. rhomboides* and juveniles of other species in our study area will be published at a later date.

It is noteworthy that, in juveniles of both *D. holbrooki* and *O. saurus*, fishes in the size range of 26 to 40 mm are the ones in which ectoparasites make their maximum contribution to the diet. Likewise, ectoparasites become markedly less important in the diets of slightly larger individuals thereby strongly implying that the cleaning habit is confined to only a portion of the total juvenile phase of development in both species. Although our data show that the diet of juvenile *O. saurus* includes proportionately greater amounts of material obtained from cleaning activities than the diet of juvenile *D. holbrooki*, it is clear that neither species depends exclusively on this activity. Limbaugh (1961) has previously reported that some species are cleaners only as juveniles and that few cleaners depend exclusively on this habit as a source of food.

Our analyses of stomach contents of *D. holbrooki* show that after reaching a length of 26 to 30 mm, this species becomes very dependent on plant material in the form of epiphytic algae. Reid (1954) found algae as well as other items in the stomachs of *D. holbrooki* from Cedar Key, Fla.; however, neither the size of the individuals analyzed nor any sort of quantitative information was reported. The study of Caldwell (1955) on this species from the same area included no information on stomach contents. Randall (1967) has reported that the diet of the closely related species, *D. caudimacula*, from the West Indies is approximately 80% algae, thereby making it quite similar in this regard to our findings with *D. holbrooki*.

Although our studies on fishes, collected in the field and obtained from museum collections, show clearly that juveniles of both *O. saurus* and *D. holbrooki* are cleaners, attempts to observe cleaning behavior in the field have been unsuccessful. The estuarine water in our study area is too turbid to permit underwater observations of the behavior of small fish at a distance. Aside from the excellent studies of Limbaugh (1964) and Hobson (1971) on cleaning symbiosis among inshore fishes of southern California, there have been few reports on visual observations of cleaning behavior by fishes in waters of the Temperate Zone. McCutcheon and McCutcheon (1964) alluded to the fact that water conditions in the Temperate Zone are frequently less favorable than those in the tropics where many detailed descriptions of cleaning symbiosis have been made. On two occasions, we observed groups of pinfish (*Lagodon rhomboides*) in our study area behaving in a manner suggestive of that described for groups of blacksmith (*Chromis punctipinnis*) when presenting themselves to a cleaner (Limbaugh, 1964; Feder, 1966; and Hobson, 1971). On both occasions, a group of several dozen subadult pinfish were seen milling about in a tight circle just beneath the surface in water approximately 6 ft deep. Pinfish are normally bottom dwellers, and the sight of a large group near the surface behaving as described above was extremely unusual. Although sizable numbers of juvenile *D. holbrooki* were seen swimming back and forth in the vicinity of the pinfish, poor visibility made it impossible to determine whether the pinfish were being cleaned. Juvenile *Diplodus* collected from this same area at this time were found to have ectoparasites (primarily *Argulus*) in their stomachs. In addition, it may be noteworthy that juveniles of *D. holbrooki* and of *L. rhomboides*, both sparids, are frequently seen swimming together in small mixed schools.

Although no observations have been made of

suggestive interspecific associations of *O. saurus*, the notes of Breder (1942) on the unusual "leaf-mimic" behavior of juveniles of this species may well be related to its cleaning behavior. Likewise the potent sting associated with the dorsal and anal spines, and the exaggerated size of these spines in juveniles (Breder, 1942), is likely to be an adaptation providing a degree of immunity from predation in this species. *Oligoplites* has not been found in the stomachs of any of the fishes we have examined even though juveniles of this species are very common in the area. We are currently investigating a change in dentition, quite likely related to the cleaning habit, which is exhibited by this species. Juveniles have an outer row of closely fitting, distinctly flattened, incisorform teeth which are seemingly well adapted to the task of scraping or of tearing objects from surfaces. In adults these teeth are more widely separated and caniform.

Limbaugh (1961) and Feder (1966) have generalized that cleaners in the Temperate Zone tend to be more gregarious and less brightly colored or contrastingly marked than cleaners in tropical waters. These generalizations have been criticized by Hobson (1969). Field observations of juveniles of both *O. saurus* and *D. holbrooki* reveal that both species are gregarious and swim about in small schools of frequently several dozen individuals. Whereas *O. saurus* is a rather unspectacular dull olive color, *D. holbrooki* possesses a bright silver sheen with a large pronounced black spot on the caudal peduncle. Hence the characteristics of these two cleaners from temperate waters provide both support and dissent to the generalizations of Limbaugh and Feder. Since *O. saurus* is also found in tropical waters, evidence of cleaning activity there would result in this species being ranked among the most unspectacularly colored of the tropical cleaners.

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COMPARISON OF VARIOUS ALLOMETRIC RELATIONSHIPS IN INTERTIDAL AND SUBTIDAL AMERICAN OYSTERS[1]

RICHARD F. DAME[2]

ABSTRACT

The allometric relationships for the possible combinations of whole weight, dry body weight, soft body weight, shell weight, height, and length were computed for intertidal and subtidal South Carolina oysters. All relationships between intertidal and subtidal oysters involving dry body weight were significantly different. The percent moisture in the tissues was 81.1% for subtidal oysters and 83.4% for intertidal oysters and did not vary with size. Height appears to be the most useful parameter for predicting other biomass parameters from field data.

The American oyster, *Crassostrea virginica* (Gmelin), is one of the principal biomass components of many southeastern estuarine ecosystems, especially that of the North Inlet Estuary, Georgetown, S.C. (Figure 1). This study of intertidal and subtidal oysters was undertaken for two principal reasons: first, quantitative estimates of various oyster biomass parameters from linear or weight measurements would facilitate secondary productivity studies; second, comparison of the morphology of intertidal and subtidal oysters from a quantitative view would give a more exact meaning to the observed differences between the two forms.

Wilbur and Owen (1964) have noted that the size relations between an intact organism and one of its parts or between two of its parts over a wide size range can usually be expressed by an allometric equation or a power function of the following form:

$$Y = aX^b. \qquad (1)$$

Y is some measure of a part, X is a measure of the whole body or another part, and a and b are constants. Equation (1) can be expressed in linear form by a logarithmic transformation as:

$$\log Y = \log a + b \log X. \qquad (2)$$

The fitted coefficients, a and b, can easily be determined from a set of data using least-squares regression techniques.

MATERIALS AND METHODS

On March 21, April 11, May 2, July 25, October 3, and December 5, 1970, groups of intertidal and subtidal (1 m below mean low water) oysters were collected from the North Inlet area. Individual oysters were separated from clumps and scrubbed with a wire brush to remove fouling organisms. The whole live weight of an individual oyster was determined to the nearest 0.01 g and varied from 1.70 to 105.50 g. The oysters were then opened, the whole bodies and shells were separated from each other, and each was dried to a constant weight in an oven at 60°C. On May 31 and July 25, the weight of each soft body was determined, and the long and short axes of each shell were measured to the nearest 0.1 mm with vernier calipers.

The statistical treatments used in this study follow the methods of Steel and Torrie (1960), and the computations were carried out on an IBM 7040 computer.[3]

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[3] Reference to trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

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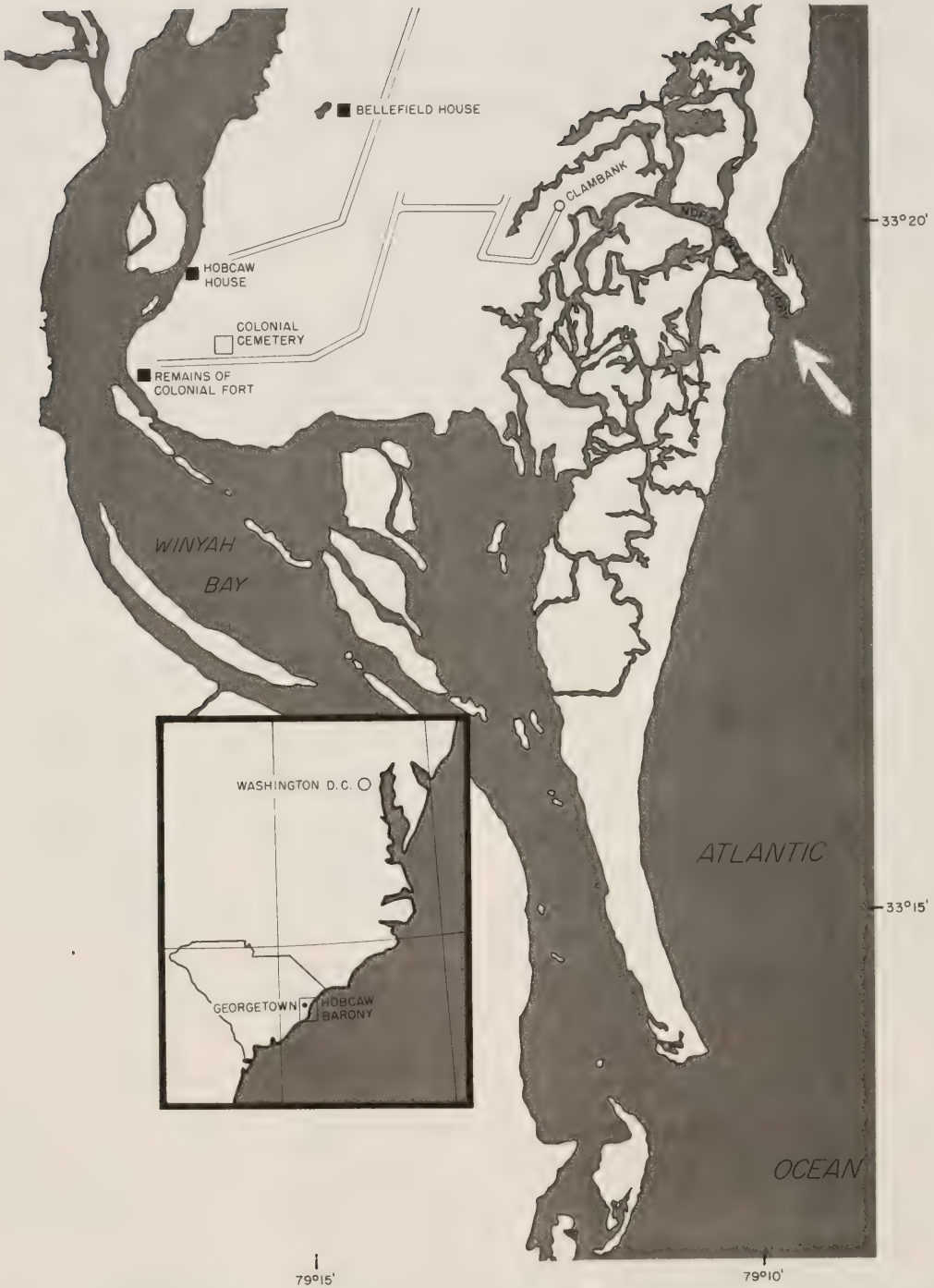

FIGURE 1.—A map showing the location of North Inlet near Georgetown, S.C.

RESULTS

Table 1 gives the allometric coefficients for Equation (2) which best fitted the observed data for the various morphological relationships. The 95% Confidence Intervals (C.I.) are included for log a and b in order to allow an indirect comparison of these values for intertidal and subtidal oysters. The coefficients of a pair of equations were considered significantly different only if the range of log a or b ± its 95% C. I. did not overlap. In addition, Table 1 gives the number of pairs of data used (n) and the coefficient of determination (r^2) which gives an estimate of how well the data fit the allometric model. (Perfect fit would be $r^2 = 1.0$.)

All relationships involving dry body weight were significantly different for intertidal and subtidal oysters.

The dry body weight/whole weight relationships for intertidal and subtidal oysters had significantly different b values, while the log a values were not significantly different. These findings mean that the growth relationships for intertidal and subtidal oysters varied with size; that is, the fitted lines are not parallel (Figure 2).

The shell weight/dry body weight relationships for intertidal and subtidal oysters had significantly different log a values, but similar b values. The subtidal ratio of shell weight/dry body weight is significantly higher than the similar intertidal relationship (Figure 2).

The dry body weight/soft body weight fitted

TABLE 1.—A comparison of the allometric coefficients for various morphological relationships for intertidal and subtidal oysters utilizing the equation log Y = log a + b log X.

Relationship $\frac{Y}{X}$	Tidal level	Coefficients ± 95% C.I.		r^2	n
		log a	b		
dry body weight / whole weight	Inter	−1.687 ± 0.044	0.960 ± 0.032	0.92	298
	Sub	−1.539 ± 0.123	0.828 ± 0.081	0.77	107
shell weight / dry body weight	Inter	1.538 ± 0.026	0.966 ± 0.045	0.90	187
	Sub	1.652 ± 0.040	0.934 ± 0.097	0.77	107
dry body weight / soft body weight	Inter	−0.779 ± 0.016	0.970 ± 0.036	0.97	80
	Sub	−0.741 ± 0.020	0.931 ± 0.042	0.97	70
dry body weight / height	Inter	−2.383 ± 0.172	2.214 ± 0.197	0.87	80
	Sub	−1.889 ± 0.198	1.794 ± 0.232	0.78	70
dry body weight / length	Inter	−1.832 ± 0.133	2.694 ± 0.258	0.85	80
	Sub	−1.465 ± 0.223	1.987 ± 0.402	0.59	70
shell weight / whole weight	Inter	−0.142 ± 0.017	1.002 ± 0.012	0.99	187
	Sub	−0.109 ± 0.038	0.992 ± 0.025	0.98	107
shell weight / height	Inter	−0.803 ± 0.140	2.301 ± 0.148	0.92	80
	Sub	−0.572 ± 0.197	2.266 ± 0.230	0.85	70
shell weight / short axes width	Inter	−0.172 ± 0.142	2.682 ± 0.274	0.83	80
	Sub	−0.105 ± 0.228	2.635 ± 0.409	0.65	70
whole weight / height	Inter	−0.689 ± 0.127	2.329 ± 0.145	0.93	80
	Sub	−0.491 ± 0.194	2.262 ± 0.231	0.85	70
whole weight / length	Inter	−0.056 ± 0.139	2.726 ± 0.270	0.84	80
	Sub	−0.008 ± 0.224	2.645 ± 0.404	0.72	70
height / length	Inter	−0.090 ± 0.085	0.689 ± 0.097	0.85	80
	Sub	−0.047 ± 0.106	0.594 ± 0.124	0.57	70
whole body weight / soft body weight	Inter	1.013 ± 0.024	0.973 ± 0.052	0.95	80
	Sub	1.038 ± 0.044	1.072 ± 0.097	0.88	70
shell weight / soft body weight	Inter	0.088 ± 0.026	0.957 ± 0.055	0.94	80
	Sub	0.092 ± 0.048	1.069 ± 0.099	0.87	70
height / soft body weight	Inter	0.739 ± 0.014	0.391 ± 0.030	0.89	80
	Sub	0.681 ± 0.024	0.414 ± 0.052	0.79	70
length / soft body weight	Inter	0.407 ± 0.014	0.309 ± 0.030	0.85	80
	Sub	0.434 ± 0.026	0.290 ± 0.054	0.63	70

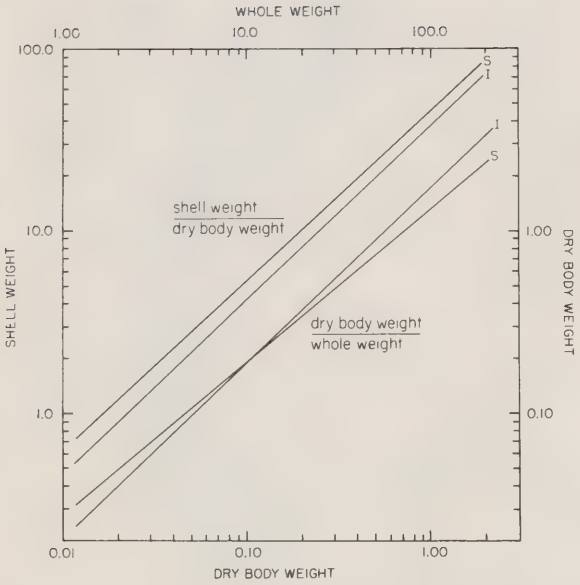

FIGURE 2.—The fitted allometric curves for the shell weight/dry body weight and dry body weight/whole weight relationships in intertidal (I) and subtidal (S) oysters.

equations had significantly different log a values (Figure 3). The ratio between dry body weight and soft body weight expresses the percent moisture in the tissues. The fitted expressions show that the percent moisture is almost constant with size since the fitted b values approach 1. The percent moisture is 83.4% in the intertidal oysters and 81.1% in the subtidal oysters.

The height/soft body weight relationships had significantly different log a values, but the b values were not significantly different (Figure 3).

The dry body weight/height relationships were significantly different in respect to their fitted log a values; the b values were not significantly different. Significantly different log a values, but similar b values indicate that the fitted curves are almost parallel (Figure 4).

The dry body weight/length relationships were the only fitted data with both significantly different log a and b values (Figure 4).

No significant differences were found between intertidal and subtidal oysters in the remaining relationships, and no significant differences were found between samples when each sample was calculated separately.

Data for subtidal oysters tended not to fit the allometric relationship as well as the intertidal oyster data. This tendency is indicated by the lower r^2 values for subtidal models, where $r^2 \times 100$ is an estimate of the percent variability of the data explained by a model. The lower r^2 values for subtidal oyster relationships may be partially attributed to the fact that fewer observations were made on this group of oysters.

DISCUSSION AND CONCLUSION

The quantitative relationships between the various parameters of weight and linear size for intertidal and subtidal oysters of different sizes have never been adequately described previously.

All significantly different relationships between intertidal and subtidal oysters involve dry body weight. Since a large proportion of the nutrients and energy available to the secondary consumers in the oyster food web is contained within the body of the oyster, this parameter is important in productivity studies. It is also important that the prediction of dry body weight

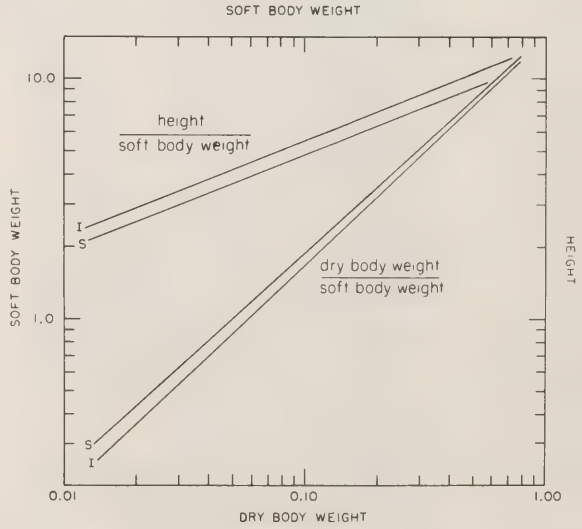

FIGURE 3.—The fitted allometric curves for the dry body weight/soft body weight and height/soft body weight relationships in intertidal (I) and subtidal (S) oysters.

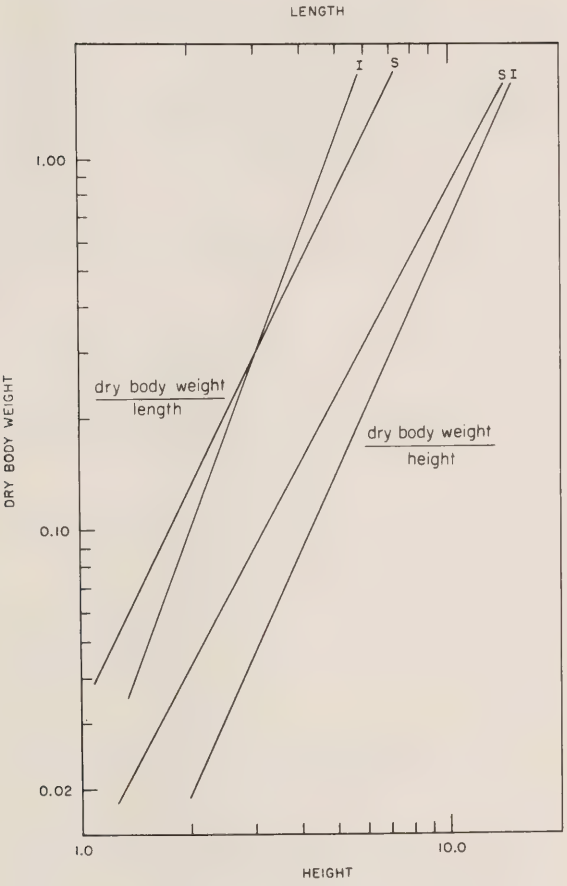

FIGURE 4.—The fitted allometric curves for the dry body weight/height and dry body weight/length relationships for intertidal (I) and subtidal (S) oysters.

from different measurements depends on significantly different models for the intertidal- and subtidal-zone oysters.

The shell weight/dry body weight ratio for *Crassostrea virginica* at North Inlet is significantly higher in subtidal oysters than in intertidal oysters. This observation supports the general observation of Galtsoff (1964) that the shells of intertidal oysters are usually thinner than those of subtidal oysters. The higher shell weight/dry body weight ratio for subtidal versus intertidal oysters is substantiated by the findings of Wilbur and Jodrey (1952), who showed that the amount of shell deposited by *C. virginica* was directly proportional to the time exposed to sea water. Rao (1953), observing a similar relationship between intertidal and subtidal *Mytilus edulis* and *M. californianus*, believed that the deposition of calcium by molluscs is directly dependent on the amount of time the animal is submerged. Baird and Drinnan (1957), finding a lower ratio of shell weight/dry body weight in subtidal *M. edulis* than in intertidal mussels of the same species, suggested that closed, exposed animals undergo anerobic metabolism which reduces body tissues more rapidly than chemical erosion of the shell. Lent (1957), discovering no differences in the shell weight/dry body weight ratio for the mussel *Modiolus demissus* from different tidal levels, attributed the result to the air-gaping phenomenon exhibited by *Modiolus*, which allows this organism to continue aerobic metabolism in both the submerged and exposed states. At present, it is doubtful if a general statement can be made that will resolve the different hypotheses. Thus, one might speculate that local environmental conditions such as tidal range, wave action, and water chemistry may be important in determining shell weight/dry body weight ratios.

In this study, the percentage water in the tissues, as calculated from the dry body weight/soft body weight relationship, falls within the reported range of 75-88% for *Crassostrea virginica* (Galtsoff, 1964). Intertidal oysters appear to retain a significantly higher proportion of their body water than subtidal oysters. The higher retention of water in intertidal oysters may result from some form of physiological adaptation to the intertidal environment, such as an increased ability to remain closed when they are exposed.

The relationships of dry body weight/whole body weight, dry body weight/height, and dry body weight/length are all different for intertidal and subtidal oysters, but there appears to be no obvious biological reason to explain these differences. It may simply be that any differences in dry body weight for intertidal and subtidal oysters are translated into differences in allometric relationships.

Galtsoff (1964) has noted that the condition index (dry body weight/volume of shell cavity

$\times$ 100) varies seasonally with the reproductive status of the adult oyster. The condition index was not measured in the present study, and no significant seasonal variations were found in any of the relationships.

It is interesting that in the present study no significant differences were found in the height/length relationships for intertidal and subtidal oysters. Glaser (1903), Orton (1936), Gunter (1938), and Galtsoff (1964) have noted differences in the long axis length/short axis width relationship for intertidal and subtidal oysters and have offered various reasons for these differences.

From the practical aspect, height appears to be the most useful parameter to predict other biomass parameters because of high coefficient of determination values in those relationships utilizing height and less time necessary to make each measurement.

In conclusion, quantitative relationships between various parameters of size can be different for oysters from intertidal or subtidal environments. These differences are important functionally in the biology of the organism and practically as predictive tools for ecological investigations.

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ACTIVITY AND FEEDING BEHAVIOR OF THE SUMMER FLOUNDER (*PARALICHTHYS DENTATUS*) UNDER CONTROLLED LABORATORY CONDITIONS

BORI L. OLLA, CAROL E. SAMET, AND ANNE L. STUDHOLME[1]

ABSTRACT

A group of five to six adult summer flounder, *Paralichthys dentatus* (Linnaeus), held under controlled laboratory conditions in a large, experimental, seawater tank, exhibited three general behavior patterns: (1) resting, (2) swimming, and (3) feeding. While resting on the sand surface, the fish maintained varying degrees of alertness, indicated by the position of the head and/or eye movements. Fish buried beneath the sand were considered to be in a lower state of responsiveness. The fish swam and glided at all levels in the water column or combined crawling and swimming to move along the sand. Activity measurements based on these swimming patterns indicated that the fish were primarily day-active. A range of feeding behaviors enabled the fish to capture prey equally well on the bottom or in the water column. The significance of these patterns and their relation to those of other flatfishes is discussed.

Until recent years, knowledge about the behavior of marine flatfishes has come mainly from the analyses of catches by fishing and research vessels to determine population structure, rates of recruitment, growth and mortality, migratory habits, and other aspects of life history from egg to adult stages. However, there are many questions that have been left unanswered, especially those concerning patterns of behavior that in many cases have a direct bearing on life habits.

One approach to answering questions on behavior is to observe the animal in the laboratory, under controlled conditions. Recent comprehensive laboratory studies on flatfishes have included work by Kruuk (1963) on *Solea vulgaris;* de Groot (1964) on *Pleuronectes platessa;* de Groot (1969) on *Solea solea, Limanda limanda, Pleuronectes platessa, P. flesus, Scophthalmus rhombus,* and *S. maximus;* and Verheijen and de Groot (1967) on *Pleuronectes platessa* and *P. flesus.* A most valuable paper by de Groot (1971) reviews the literature and discusses food, feeding behavior, and activity in flatfishes. These investigations have pointed to the diversity of their habits and the importance of comparative studies in understanding the interrelations between the various species.

In this work we have endeavored to further the understanding of some specific behaviors by studying, under controlled laboratory conditions, the activity cycles, feeding, and general swimming patterns of adult summer flounder, *Paralichthys dentatus* (Linnaeus), a species of major commercial and recreational importance.

MATERIALS AND METHODS

We observed five to six adult summer flounder, captured 16 to 48 km off the coast of Maryland. The fish ranged in length from 37.0 to 74.5 cm and in weight from 957.0 to 5,690.0 g.

We held the fish in an elliptical seawater aquarium, 10.6 × 4.5 × 3.0 m deep with a capacity of 121 kliter (Olla, Marchioni, and Katz, 1967). To provide a suitable bottom habitat for the fish, we added several layers of gravel, covered by an upper layer of 0.6 to 0.8 mm sand. Beneath the sand and gravel was a network of

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pipes designed to move filtered water through the layers to prevent contamination of the bottom. Water temperature in the tank ranged from 17.0° to 20.0°C. Salinity ranged from 23.0 to 26.0‰, oxygen from 6.5 to 7.7 mg/liter, and pH from 7.3 to 7.7.

Fluorescent lights mounted on two side walls above the aquarium were mechanically timed to approximate the natural daily photoperiod from morning to evening civil twilight. Since Verheijen and de Groot (1967) reported that high light intensities could inhibit normal activity in flatfish, we held the maximum daytime light intensity, as measured at the surface, at 3.5×10^2 mc. Preliminary measurements showed this level not to be inhibitory. An automated dimming system gradually raised and lowered light intensity during morning and evening civil twilight, avoiding sudden light changes that might startle the fish. A second lighting system, which switched on before the dimmer lights were extinguished, provided an indirect light of 2×10^{-1} mc as measured at the water surface (2.5×10^{-3} mc at 1 m below the surface) during the night period.

Throughout the course of the observations, at intervals of about 30 days, we fed the fish 1,100 to 4,400 g of live sand shrimp, *Crangon septemspinosa*, and grass shrimp, *Palaemonetes vulgaris*. The quantity of shrimp introduced each time insured a food supply which lasted for 30 days. According to Poole (1964) and Smith (1969), shrimp appear to be an important constituent of this species' natural diet.

Following 34 days of acclimation to the tank, we measured the activity of six fish over a 51-day period. At the end of this time, one fish died and our measurements were then based on five fish. Throughout the day and night, we made 5-min observations every hour 4 days each week of the number of fish swimming, feeding, or moving about on the bottom.

We found that 5 min was too brief to allow for extensive observations of the fish's behavior, so after establishing the daily cycle of activity, we lengthened these periods to 30 min every 3 hr 4 days each week. In conjunction with these extended observations, we periodically took motion pictures which allowed us to make a more detailed analysis of feeding and swimming. Gliding and swimming speeds were measured from these motion pictures as well as from stopwatch readings taken as the fish passed between two marks 335 cm apart.

RESULTS

We have classified the activity patterns of the fish into three general categories: (1) resting, either on the surface of the sand or beneath it, (2) swimming, and (3) feeding. Within these three categories, we have described the various aspects of each behavior in an attempt to provide a clearer picture of the fish's habits.

RESTING

The summer flounder exhibited three basic resting positions: (1) lying flat on the sand; (2) lying on the sand with the head raised (as much as 7.5 cm), supported by the body musculature and the anterior portions of the dorsal and anal fins braced vertically into the sand; and (3) buried beneath varying amounts of sand.

In the first resting position, while flat on the sand, the eye turrets were either retracted or extended. When extended, the eyes either remained relatively fixed or moved up to 6 to 8 times per min. When the head was raised, as in the second resting position, eye movements were generally more frequent, ranging from 10 to 30 times per min, reflecting a higher degree of responsiveness. This "head-up" posture was generally characteristic of an animal at a higher level of activeness than fish lying flat.

Fish in either resting position occasionally "yawned." The head was elevated, the mouth opened, and the opercula extended. Yawning occurred either as a single event or up to 16 times in rapid succession. As yawning was repeated, the gape of the mouth increased and the head rose progressively farther off the sand. During the 30-min observation periods, we recorded the events preceding and following 33 yawns, i.e., separate occurrences, whether comprised of a single yawn or a number of successive yawning movements. Of these, 24 preceded an immediate

change in activity; i.e., 17 times yawning preceded swimming from a resting position, 2 times it preceded burying, and 5 times, a change in position. In seven instances, 5 to 10 min elapsed, before the fish proceeded to bury (2 times), swim (4 times), or change position (once). The remaining two instances occurred as the fish settled on the sand after swimming. It appeared from these findings that yawning generally was associated with changes in activity. This is similar to the increased activity following yawning in the yellowtail demoiselle, *Microspathodon chrysurus*, (Rasa, 1971).

The buried position was characteristic of fish in a state of low responsiveness, similar to that shown by fish lying flat on the surface of the sand. The eyes seldom rotated and a buried fish did not respond to prey that moved or settled directly within its line of vision. Burying began with an upthrust of either head or tail which continued as a beating of the head and tail alternately against the sand, from 5 to 10 times, until the fish was partially or completely covered. This took 1.5 to 3.0 sec.

The events leading to burying were apparently nonspecific. For instance, after swimming, some flounder would settle on the sand and immediately bury. Other flounder resting on the sand for as long as 20 min would, for no reason apparent to the observer, bury. We also found that, as described below, burying might occur as a secondary response when the fish were subjected to an intense or sudden stimulus.

SWIMMING

Swimming movements could begin from any resting position and could be classified into three categories. In one category, fish swam in the water column, at any depth from surface to bottom, at speeds ranging from 19.0 to 58.0 cm/sec. As a fish swam, the head moved up and down while the body musculature expanded and contracted, the whole process viewed as a series of rhythmic undulations. The caudal fin exerted most of the momentum for forward movement; the left pectoral (the eyed side) and to a lesser extent, the right pectoral, acted as rudders. To counteract their natural negative buoyancy, and hence the tendency to sink, the fish were continually in motion, swimming at one level or swimming upward.

A second type of swimming combined active propulsion and gliding. The fish would swim upward in the water column (Figure 1A and B) and then, by positioning the head downward and

FIGURE 1.—Swimming and gliding behavior. A swimming fish (A, B) flexes from head to midsection (C) to begin a glide. As the head drops (D) and the body flattens (E), the fish glides downward and forward (F, G). At any depth, the fish can either resume swimming (H) or brake its forward glide (I).

flattening the body, would glide downward and forward (Figure 1C-H). The angle and rate of descent were controlled by the position of the head and body relative to the bottom as well as by the position of the dorsal, anal, and caudal fins. By raising the pectoral fins and posterior portions of the dorsal and anal fins, while simultaneously lowering the anterior portions of the dorsal and anal fins and arching the body, the fish could brake its forward motion in midwater (Figure 1I), either to change swimming direction or to approach a potential prey. Gliding was an effective means of covering distances while in the water column. Starting at a height of 1.8 m from the bottom, a fish could glide 4.5 to 6.5 m at speeds ranging from 34.0 to 64.0 cm/sec.

A third type of swimming combined swimming within 5 to 15 cm of the sand and crawling ("shambling" as described by Kruuk, 1963; and Verheijen and de Groot, 1967). This was most often observed when the fish were actively seeking prey. Shambling speeds ranged from 32.0 to 48.0 cm/sec.

ACTIVITY CYCLE

Based on hourly counts of the number of fish swimming in the water column or moving along the sand, we found the flounder to be primarily day-active (Figure 2A-H) although the light level at night was apparently sufficient to permit swimming and feeding.

Throughout the course of our observations, there was an overall decrease in activity occurring first at night (Figure 2B) and then during the day (Figure 2E-H). During this time, the photoperiod was changing, approximating the natural seasonal daylength. While changing photoperiod may act as an assignable cause for the decline in the fish's activity, observations included only a small part of the natural seasonal photoperiod cycle, too brief a time to permit a definitive statement as to its influence on activity.

FEEDING

The fish could feed with as much facility on the bottom as in the water column. Bottom

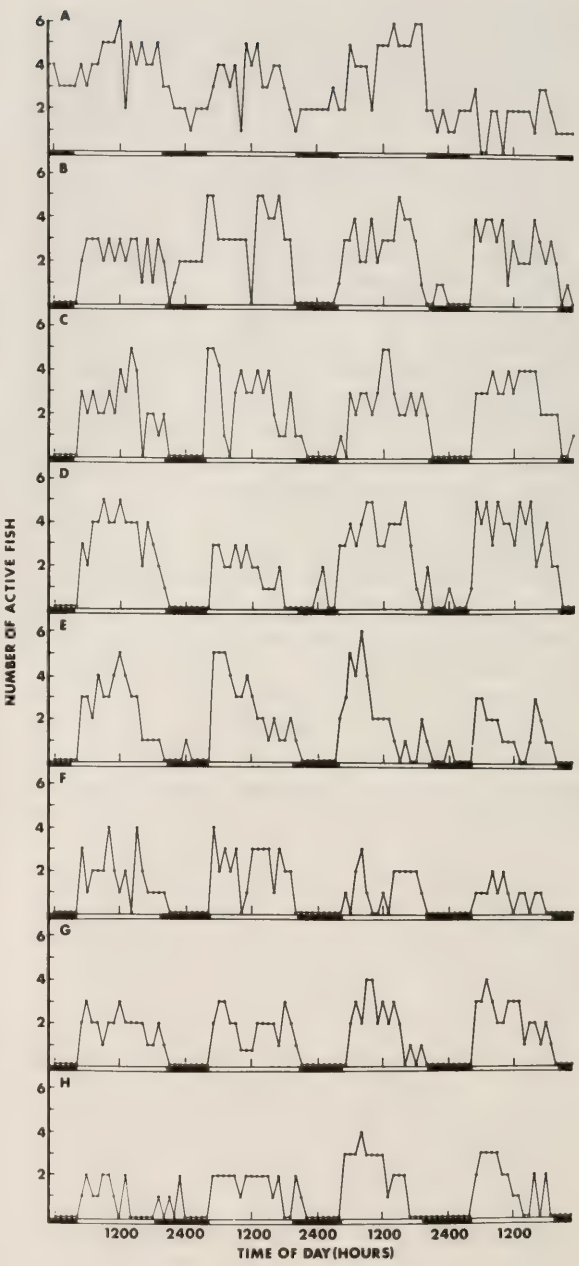

FIGURE 2.—Number of fish swimming in the water column or moving along the sand. Counts were taken at hourly intervals throughout the day and night under the following average photoperiods: (A) 16.3 hr; (B) 16.4 hr; (C) 16.4 hr; (D) 16.3 hr; (E) 16.2 hr; (F) 16.0 hr; (G) 15.9 hr; (H) 15.8 hr.

feeding was always preceded by active prey search. In most instances, a flounder, after selecting a potential prey, would rest on the sand with the head slightly raised. Then, while visually fixing on a shrimp, the fish would begin to stalk, crawling on the sand towards the prey. This crawling was viewed as waves of cephalocaudal movements of the dorsal and anal fins (Figure 3A-D). When a fish was within striking distance (5-10 cm), the head was angled downward or lay flat on the sand. The midsection of the body was arched, supported by the caudal fin and by portions of the edges of the dorsal and anal fins braced into the sand (Figure 4A). As the caudal fin beat downward (Figure 4B), the fish sprang forward, mouth agape and opercula spread, striking and ingesting the shrimp (Figure 4C). Speed during the strike was about 40 to 50 cm/sec. After ingestion, there was continued mouth movement, apparently part of the pharyngeo-esophageal activity necessary for swallowing.

Fish that were resting on the bottom, with the head either up or down, would not strike at shrimp even though prey were well within striking distance. Feeding was always preceded by active search, although these fish were seemingly well-adapted for a "lying-in-wait" method of prey capture.

Fish swimming 50 to 70 cm above the bottom could also capture shrimp from the sand. As a swimming fish (Figure 5A) visually fixed on a single shrimp, speed abruptly decreased (Figure 5B). While the flounder was still moving forward, it would tilt towards the sand at a 30° to 45° angle. At this point, with the prey about

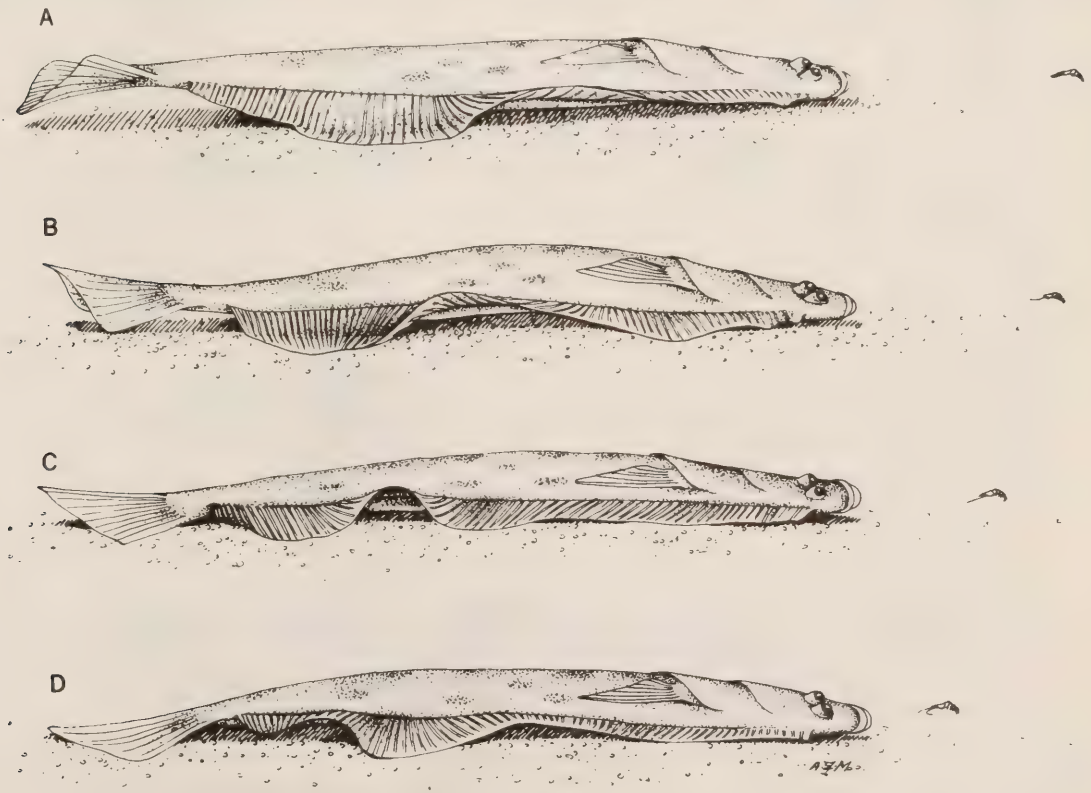

FIGURE 3.—Stalking behavior. The fish visually fixes on a shrimp and crawls slowly forward on the dorsal and anal fins (A-D).

20 cm away, its forward motion almost ceased. Then, when within 3 to 5 cm of the prey (Figure 5C), the fish beat downward with the caudal fin and with mouth agape and opercula spread, moved forward and downward. As the fish ingested the shrimp, it would usually make contact with the bottom with its snout, then glance off the sand, and move slightly forward and upward (Figure 5D). The fish would then resume swimming or settle on the sand.

The basic elements of prey selection and visual fixation were essentially the same whether the fish were feeding in the water column or on the bottom. While the flounder were actively swimming or gliding toward shrimp, they would approach and decrease speed by raising posterior portions of the dorsal and anal fins and arching the body into a partially flexed position. Then, with a rapid caudal flexion, the fish would capture and ingest the shrimp. As was the case with bottom feeding, after capturing a prey, a fish would either continue active search or settle on the sand.

The searching, stalking, active eye movements, and visual fixation on specific prey all indicated that vision was a primary sense used in feeding during the day. We observed feeding at night, and while it appeared to us that the role of vision was similar to that in the day, we could not preclude the possibility of other senses playing more dominant roles.

At times the flounder would approach a prey, as if to begin stalking or a capture, but would then turn away. We considered this type of behavior to be a feeding intention movement. For example, a flounder would swim toward shrimp on or near the bottom, assume a prestrike posture, visually fix on a shrimp, and open and close

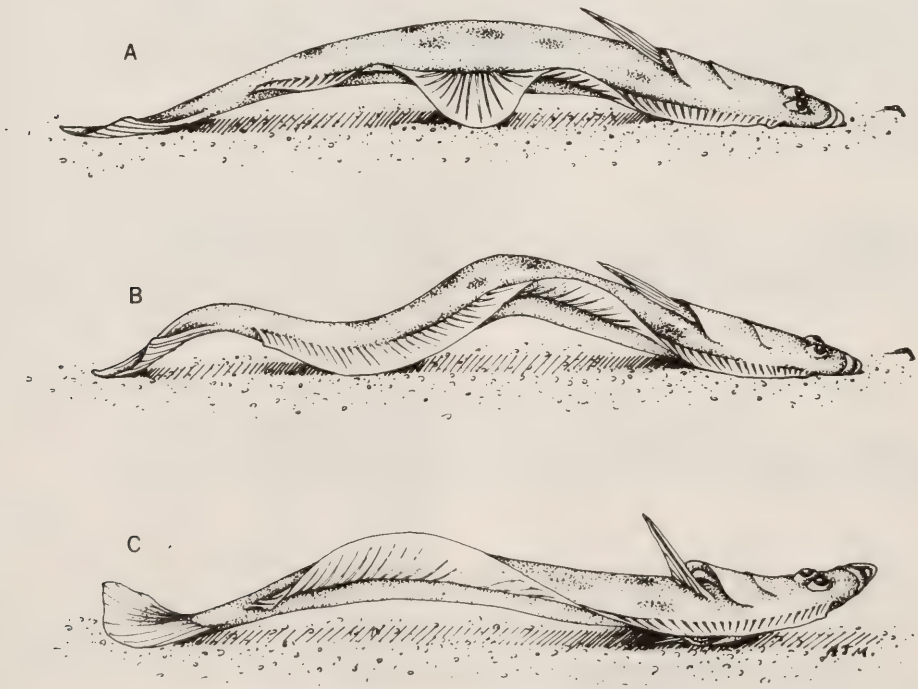

FIGURE 4.—Prey capture following stalking. The fish assumes a position prior to striking. The body is slightly raised off the sand and the eyes are visually fixed on the prey (A). As the strike begins, the caudal fin beats downward (B), thrusting the fish forward for the capture (C).

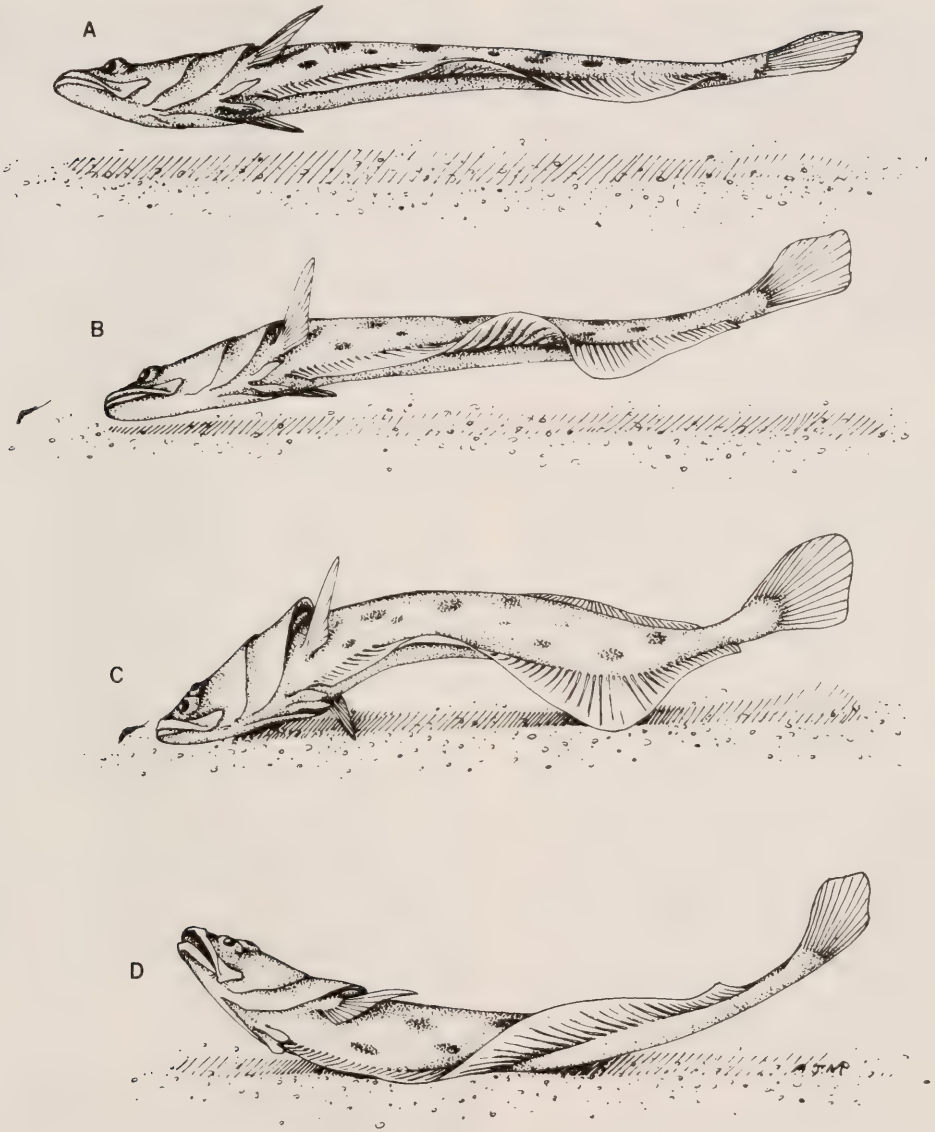

FIGURE 5.—Bottom feeding by a swimming fish. A swimming fish (A) visually fixes on a shrimp on the bottom, partially brakes its forward motion (B), and tilts toward the sand. As the caudal fin beats downward, the mouth opens, the opercula spread, and the fish moves ahead to ingest the shrimp (C, D).

its mouth several times. Then, without lunging or striking at the prey, the fish would swim away after a few seconds.

We found feeding intention movements to occur after the fish had been feeding. For instance, in one case, after we had introduced 1,100 g of shrimp into the tank (29 days after the last feeding of 4,400 g of shrimp), the fish began to feed within 3 min. One fish, after eating 13 shrimp within a 22-min period, exhibited

an intention movement 3 min later. Then four more shrimp were ingested during the next 20 min, followed 2 min later by two additional intention movements. A second fish ingested 15 shrimp within 35 min and 2 min later made an intention movement. A third fish, after ingesting 16 shrimp in 26 min, made an intention movement 1 min later, then fed immediately on one shrimp, and 2 min later exhibited an intention movement. These movements may have been related to a reduction of feeding motivation as a result of satiation.

FRIGHT RESPONSE

We observed what was apparently a "fright" response to a sudden stimulus under two different circumstances. In one case, there was a malfunction of the dimmer lights which caused the sudden onset of the daylight lights. A swimming fish immediately dropped to the bottom where it remained resting on the sand surface. In another case, an observer above the tank waved his arms as a fish moved about near the water surface. The fish immediately dropped to the sand, darkened, and assumed a rigid posture. The head and caudal fin lay flat, but the dorsal and anal fins were arched in two places along their length. The fish remained in this posture for about 45 sec during which it slowly lowered first the anterior, then the posterior sections of the dorsal and anal fins until they were flat. The flounder then swam about 2 m away and buried. In both instances, the initial response of the fish to a fright stimulus was to drop to the bottom and remain motionless. Burying occurred as a secondary response.

DISCUSSION

Previous descriptions of the habits of summer flounder have characterized them as primarily bottom-oriented, except for occasional sorties to the surface in pursuit of prey (Bigelow and Schroeder, 1953:267-270). Furthermore, this species has been described as being relatively immobile, except while feeding or during the normal migratory period (Ginsberg, 1952). In our laboratory observations, while the fish frequently searched for and captured prey on the sand and also remained quiescent on the bottom for long periods, they would also frequently use the water column for swimming, prey search, and feeding. In fact, during one part of our study, the fish swam and glided for extended periods throughout all levels of the tank, seldom resting in any one position.

The gliding behavior we observed could play an important role for the animal in the sea. After reaching the surface, the fish could travel considerable distances with little or no active swimming movements, using natural negative buoyancy and body shape to full advantage. Positioning of the fins and body would control forward speed and distance traveled. Although there might have been a sacrifice in speed, the gliding would represent a saving in energy as compared with that required to swim the same distance. Gliding would also enable the animal to search for and capture prey in the water column more efficiently, since it could approach a prey with less gross movement than would occur during active swimming. This might lessen the chance of eliciting escape responses from the prey due to visual or mechanical stimuli. Another adaptive advantage of gliding in food search might be related to the fact that the head was steady, thus making it easier to keep the prey in the visual field.

Although the summer flounder were primarily day-active, we observed burying, feeding, shambling, and swimming both day and night. Similar to the summer flounder, turbot (*Scophthalmus maximus*) swim and are active on the bottom primarily during the day, although both activities may occur at night to a lesser degree (de Groot, 1971). Verheijen and de Groot (1967) and de Groot (1971) established that plaice (*Pleuronectes platessa*) and flounder (*P. flesus*) showed a nocturnal pattern of swimming in the upper water column, while during the day they would shamble or swim over the bottom searching for food. Kruuk (1963) and de Groot (1971) found that the sole (*Solea vulgaris*) also had a nocturnal period of high activity under both natural and artificial light.

The method of burying in the summer flounder is similar to Kruuk's (1963) description of "digging-in" in the sole. In the sole as well as the

winter flounder, *Pseudopleuronectes americanus,* (McCracken, 1963) and starry flounder, *Platichthys stellatus,* (Orcutt, 1950), burying could be induced as a direct response to a sudden disturbance, such as a change in light intensity or moving object. In the summer flounder, apparently the primary response to a fright stimulus is to assume a stationary and sometimes rigid posture on the bottom. This is followed by burying as essentially a secondary response.

There are numerous descriptions of the sensory mechanisms utilized by different groups of flatfishes during feeding (see de Groot, 1971, for review). Since summer flounder are primarily day-active, it was not surprising that vision played a primary role in prey selection and capture. According to de Groot (1971), this is apparently characteristic of Bothidae including brill (*Scophthalmus rhombus*) and turbot, which he designated as visual day-feeders, largely dependent on visual stimuli for locating prey. Despite the fact that the summer flounder would also be categorized in this manner, we did observe feeding at night. Although the light level of 2.5×10^{-3} mc (as measured at 1 m below the surface) fell slightly below the 10^{0}-10^{-2} mc level cited by Blaxter (1970) as the range in which most visual feeders cease active feeding, it was possible that vision was still being utilized.

The summer flounder, winter flounder, (Olla, Wicklund, and Wilk, 1969), and lemon sole, *Microstomus kitt,* (Steven, 1930) may rest on the bottom with head up while actively moving their eyes. In the latter two species, the fish may be searching for food and will lunge forward from this position to strike at and capture prey. While we considered summer flounder in this position to be alert and responsive, it was also apparent that this was not necessarily indicative of a prefeeding strike. Although Ginsberg (1952) stated that summer flounder lie in wait for passing prey, we found that the fish, even in this alert "head-up" posture, never lunged from a resting position at a prey, even though it was only a few centimeters away, but always preceded prey capture by active searching.

While we do not understand the role yawning plays in the behavior of the summer flounder, we did find evidence that it was associated with changes in activity. Rasa (1971) found that yawning in the yellowtail demoiselle was associated with an increased excitement level. She postulated that the strong muscle contraction that occurs during yawning could serve to increase the blood flow and oxygen to the body musculature and thereby facilitate the onset of the animal's activity. It may also be conceivable that yawning movements may act to flush sand or debris from the gill areas, one function suggested for yawning in Pacific bonito, *Sarda chiliensis,* (Magnuson and Prescott, 1966).

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THE EFFECTS OF TEMPERATURE AND PHOTOPERIOD ON REPRODUCTIVE CYCLING IN THE ESTUARINE GOBIID FISH, *GILLICHTHYS MIRABILIS*

VICTOR L. DE VLAMING[1]

ABSTRACT

Investigations were undertaken at several different times during the year to examine the effects of various photoperiods and constant-temperature regimes on reproductive function in the longjaw goby, *Gillichthys mirabilis*, with the intent of evaluating the influence of these factors in regulation of the annual sexual cycle. Testicular regression occurs at any time during the year when fish are exposed to constant temperature of 24°C and above, independent of photoperiod. Similar results were obtained with female fish, but 22°C is the thermal threshold. It is concluded that the gonadal regression observed in the Alviso population of this species during the summer months is a consequence of increasing temperature. At high temperatures, the transformation of spermatogonia to spermatocytes is blocked, and in females vitellogenesis is inhibited. The degree of gonadal regression is temperature-dependent. Gonadal recrudescence is dependent on low temperatures (10°-20°C) and will not occur if fish are exposed to high temperatures (24°C or above) regardless of photoperiod. At low temperatures, short photoperiods accelerate recrudescence. Between January and June spermatogenesis and oogenesis are maintained at temperatures between 10° and 21°C; long photoperiods are more effective in this respect, but not essential. Termination of the reproductive season in this species is not endogenously timed. Regression is not "obligatory" since gonadal involution does not occur at the "normal" time if fish are exposed to temperatures of 20°C or below.

The survival of any species in a seasonally changing environment is dependent on the development of mechanisms that permit it to adjust physiological functions to changes in the environment. Studies of reproductive timing and how the environment influences this timing are of importance in understanding the ecology of any species.

Compared with the wealth of information available on the systematics, ethology, and physiology of fishes, there is little knowledge concerning how external factors regulate their reproduction. Some investigations have been undertaken to elucidate the role of environmental factors in regulating the reproductive cycles of various teleosts. The relationship of environmental factors to the reproductive cycles of gobies has not received experimental consideration. Moreover, experimental work with the environmental control of teleost reproductive cycles has been confined to fewer than 20 species representing only 8 families.

Photoperiod and temperature are presumed to be the most important factors (i.e., the most studied) influencing the neuroendocrine centers that control gonadotropin secretion in teleosts (de Vlaming, 1972a). The experimental conditions employed in a majority of the previous studies, however, are diverse and the results contradictory. In fact, most of the experimental work was too poorly controlled and too brief in duration to allow proper assessment of the role of the environment in synchronizing fish reproduction (de Vlaming, 1972a).

The subject of the present study is the longjaw goby, *Gillichthys mirabilis*. It is distributed

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from central California south to Magdalena Bay, Baja California, and the Gulf of California south to Mulegé on the west coast, and south to Agiabampo Bay on the east coast (Barlow, 1963). The typical habitat of this species is the intertidal region of coastal sloughs. Barlow (1961, 1963) discussed the systematics and some aspects of the ecology of *G. mirabilis*. The population of *Gillichthys* used in these studies occurs in the Alviso salt ponds located at the southern end of San Francisco Bay, Calif. Carpelan (1957) described seasonal changes in the hydrobiology of these ponds.

De Vlaming (1972b) described the reproductive cycle of *G. mirabilis* and suggested that seasonal temperature changes may be involved in regulating sexual cycling in this species. The spawning period is protracted, extending from December to June. Gonadal regression occurs in July; the gonads remain regressed during August and September. Gonadal recrudescence begins in late September, reaching completion by early December.

The aim of the present study was to determine the effects of various light and constant temperature regimes on gonadal function in *G. mirabilis*, with the hope of evaluating the influence of these factors in regulation of the annual sexual cycle. The phenological data on reproductive cycling in this species presented by de Vlaming (1972b) was used as a basis for these studies. Some of the previous studies with teleosts have shown that the effect of the environmental synchronizer(s) varies with the stage of gonadal maturity. Consequently, the effects of photoperiod and constant temperature treatments were examined during different phases of the gonadal cycle.

MATERIALS AND METHODS

Samples of *G. mirabilis* were captured in the Alviso habitat at several different times during the year and thus in different phases of gametogenesis. Since males were more abundant in these samples, a greater number of experiments were conducted with this sex. Several fish from each sample were sacrificed, and the gonads examined at the time of capture; these fish served as a reference for the experiments that followed. In the following discussion the fish sacrificed from the samples from nature will be referred to as initial controls. In many of the experiments, samples of fish from the natural habitat were collected and sacrificed upon termination of the experiment; these fish will be referred to as terminal controls. To facilitate quantification of gonadal response, animals of approximately equal size were utilized in these experiments.

Experimental fish were maintained in 56- (no more than 10 fish per tank) or 132-liter (no more than 18 fish per tank) tanks. Recirculating filtered seawater was used in all of these experiments. The bottom of each tank was covered with fine gravel. The experimental tanks were housed in constant temperature rooms ($\pm$ 1.5°C). Temperatures selected for these experiments are within the range normally experienced by this species during the year.

Various photoperiods were also employed in these experiments. Light was provided by 20-w warm-white fluorescent bulbs suspended above the tanks. Salinity was maintained at a constant 35 ‰, and pH between 8.0 and 9.5 (these pH's are consistent with those experienced by the fish in the Alviso ponds). The fish in these experiments were provided with a varied diet consisting of brine shrimp, chopped fish, boiled egg white, and beef kidney and liver; all fish ate voraciously.

Upon termination of each experiment, the weight and standard length of each fish were recorded. Gonads were weighed and prepared for histological examination in the same manner as previously reported (de Vlaming, 1972b). Gravimetric data are expressed in absolute weights since it was shown (de Vlaming, 1972b) that gonadal weight is independent of body weight (and length) in the size range used. Spermatogenesis and oogenesis were divided into six and five recognizable phases (Tables 1 and 2) to facilitate quantitative evaluation of gametogenetic activity.

Statistical comparisons of gonadal weights between experimental groups were made by using the Mann-Whitney *U* test (Siegel, 1956, p. 184-193). This nonparametric test is suitable for small sample sizes and can be used to determine

TABLE 1.—Criteria used for histologically staging testes of *Gillichthys mirabilis*.

Stage	Histological characteristics of testes
0	"Regressing testis." Seminiferous lobules characterized by large numbers of pyknotic nests of degenerating cells (spermatozoa, spermatids, and spermatocytes); phagocytes observed free within the lobules.
1	"Quiescent testis." Seminiferous lobules small in diameter. Germinal epithelium consists of only spermatogonia. Lumen of the lobules contain only few residual spermatozoa, and the sperm duct is collapsed.
2	"Mitotic phase." Same as Stage 1, with the exception that mitotic figures are observed in the spermatogonia.
3	"Meiotic phase or active spermatogenesis." Testicular lobules larger than in Stages 1 and 2; germinal epithelium consists of spermatogonia, spermatocytes, and spermatids.
4	"Prespawning testis." Seminiferous lobules large and distended with sperm. Germinal epithelium consists of relatively few spermatogonia.
5	"Postspawning testis." Seminiferous lobules small and contain relatively few sperm; sperm duct expanded and containing residual sperm.

TABLE 2.—Criteria used for histologically staging ovaries of *Gillichthys mirabilis*.

Stage	Histological characteristics of ovaries
I	"Regressing ovary." Atretic follicles predominate in the ovary. Only nonyolky oocytes and oogonia present.
II	"Quiescent phase or phase of oogonial proliferation." Ovary characterized by nonyolky oocytes with a basophilic cytoplasm, and a diameter of less than 75 μ. Granulosa not fully organized around the developing oocytes.
III	"Phase of active vitellogenesis." Ovary characterized by developing yolky oocytes whose diameter is between 75 μ and 640 μ. Granulosa fully organized around the oocytes.
IV	"Prespawning condition." Ovary characterized by oocytes whose diameter is in excess of 640 μ. Yolk vesicles abundant.
V	"Postspawning condition." The ovary is wine-red in color; the tunica albuginea thick, highly vascularized, and folded. Postovulatory follicles predominate in the ovary. The stroma of the ovary appears disorganized, yet highly vascularized.

whether two independent groups have been drawn from the same population.

RESULTS

EFFECTS OF CONSTANT TEMPERATURE AND PHOTOPERIOD ON FISH WITH REGRESSING GONADS

To examine the influence of low and high temperature treatments at different photoperiods on gonadal recrudescence, fish with regressing testes (Stage 0) and ovaries (Stage I) were collected in July 1967. Fish were exposed to 13°C, at a short (8L/16D) or long (15L/9D) photoperiod, or to 27°C at a short photoperiod (8L/16D).

The effects of these treatments on testicular and ovarian weights are summarized in Figure 1. The testes (Stage 0) and ovaries (Stage I) of all of the initial controls were regressing. After 57 days, testicular and ovarian weights increased significantly ($P < 0.01$) at both photoperiods at 13°C, and were also significantly greater ($P < 0.01$) than those of fish from nature sacrificed at the same time. Ovarian weights of females exposed to 8L/16D at 13°C were significantly greater ($P < 0.01$) than those of fish exposed to 15L/9D at the same temperature.

Testes of all fish at 13°C were in the meiotic phase of spermatogenesis (Stage 3) whereas those of all fish in the September sample from nature were only in Stage 2 (mitotic proliferation phase). The ovaries of all fish at 13°C were in phases of vitellogenesis (Stage III); the oocytes of fish at 8L/16D were, however, in a

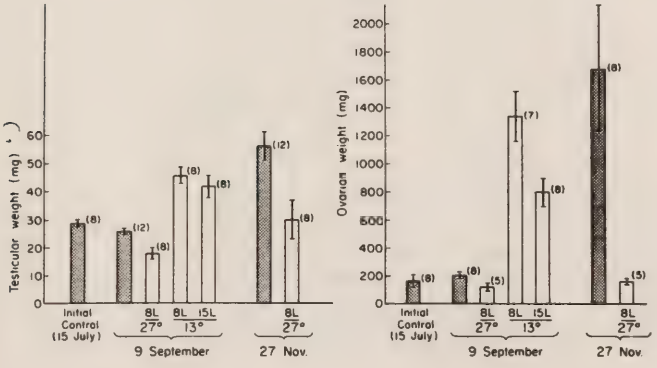

FIGURE 1.—Effect of 13°C at a long (15L/9D) photoperiod and 13° and 27°C at a short (8L/16D) photoperiod on testicular and ovarian weight in *Gillichthys mirabilis*. Mean gonadal weight is illustrated by histograms; the mean is bracketed by one standard error. Shaded histograms represent gonadal weight of samples collected in nature; open histograms, experimental groups. Light (hours per 24 hr), temperature, and dates on which fish were sacrificed are recorded below the histograms. Sample sizes are indicated atop each histogram.

later stage of vitellogenesis. The ovaries of all fish in the September nature sample were in the quiescent phase (Stage II).

After 57 days at 27°C, testicular weights were significantly lower ($P < 0.05$) than those of the initial July controls. The testes of all fish were in the quiescent phase (Stage 1), even after 134 days. In contrast, the testes of all fish in the November sample from nature were in Stage 3.

Ovarian weights of fish exposed to 27°C (both the September and November samples) did not differ significantly from those of the initial July controls, but they were significantly lower ($P < 0.01$) than ovarian weights of both 13°C groups. The ovaries of the 27°C treated fish revealed only resting oocytes (Stage II). However, the ovaries of fish in the November sample from nature were in Stage III, IV, or V.

Thus, low temperatures promote gonadal recrudescence in *Gillichthys*, independent of photoperiod. Short photoperiods may accelerate the rate of gonadal recrudescence at low temperatures. A short photoperiod, however, failed to initiate gonadal recrudescence at high temperature. High temperatures act by blocking vitellogenesis and the transformation of spermatogonia to spermatocytes.

The influence of constant temperature and photoperiod on testicular recrudence was examined again in July 1968, using 13° or 20°C, with a short (8L/16D) and a long (15L/9D) photoperiod. A fifth group was exposed to 24°C at a long photoperiod (15L/9D). Each group was sampled after 45, 70, and 120 days (Figures 2 and 3).

In the initial July controls testes were regressing (Stage 0). At 24°C testicular weights remained low throughout the experiment; in September and November testicular weights at this temperature were significantly lower ($P < 0.05$) than those of the initial July controls. Moreover, at 24°C testes remained in the regression or quiescent phase (Stage 0 or 1) throughout the experiment (Figure 3).

At 20°C testicular weights remained essentially the same as in the initial July controls

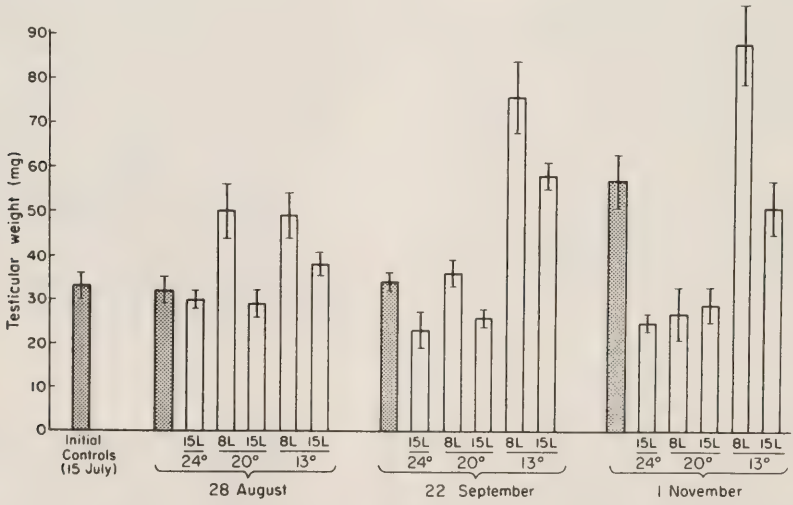

FIGURE 2.—Effect of 24°, 20°, and 13°C treatments at short (8L/16D) and long (15L/9D) photoperiods on testicular weight in *Gillichthys mirabilis*. Mean testicular weight is represented by histograms; the mean is bracketed by one standard error. Shaded histograms represent testicular weight of samples collected in nature; open histograms, experimental groups. Light (hours given per 24 hr), temperature, and dates on which fish were sacrificed are recorded below the histograms. For sample sizes, see Figure 3.

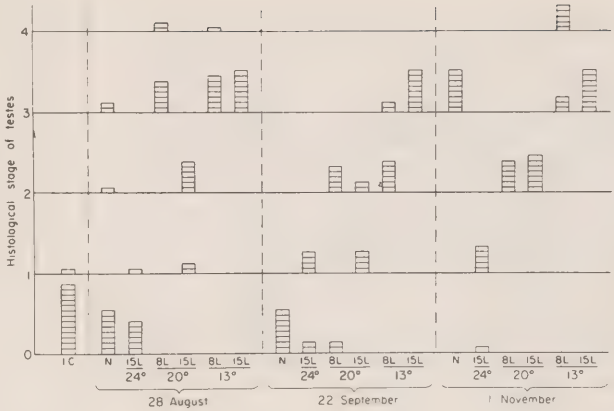

FIGURE 3.—Effect of 24°, 20°, and 13°C treatments at short (8L/16D) and long (15L/9D) photoperiods on testicular histology in *Gillichthys mirabilis*. I.C. refers to initial controls (15 July) and N, to samples from natural population. Each box represents the testicular condition of one fish.

with one exception. Testicular weights of the 20°C group at 8L/16D sacrificed in August were significantly greater ($P < 0.05$) than those of the July controls. With the exception of this same group, active spermatogenesis was not initiated in fish exposed to 20°C. Mitotic proliferation of spermatogonia was, however, stimulated by this treatment. In contrast, active spermatogenesis was initiated by August at 13°C, regardless of photoperiod. Active spermatogenesis was not initiated in the natural population until after 22 September. Testicular weights of both groups at 13°C sacrificed in September were significantly greater ($P < 0.01$) than those of the initial July controls and those of the September sample from nature. Some photoperiod effect was evident at 13°C since testicular weights at 8L/16D were significantly higher ($P < 0.05$) than those of the 15L/9D group by September. By November, the testes of a majority of the fish in the 13°C-8L/16D group were in the prespawning condition (Stage 4) whereas the testes of all fish in the 13°C-15L/9D group were in Stage 3; testicular weights of these two groups were also significantly different ($P < 0.01$).

These data indicate that 24°C inhibits testicular recrudescence by blocking the transformation of spermatogonia to spermatocytes and also retards mitoses in the spermatogonia. Low temperatures promote testicular recrudescence; the rate of recrudescence at a low laboratory temperature was faster than in the natural population. At low temperatures, short photoperiods accelerate testicular recrudescence. With the exception of the one sample at 20°C-8L/16D sacrificed in August, 20°C stimulates little or no testicular recrudescence, only mitotic proliferation of spermatogonia.

EFFECTS OF CONSTANT TEMPERATURES AND PHOTOPERIOD ON FISH IN STAGES OF ACTIVE GAMETOGENESIS (MAY)

Responses of fish in phases of active gametogenesis (in May) were examined by exposing two groups of fish for 67 days to 13°C, at a short (8L/16D) and a long (15L/9D) photoperiod, and 27°C at a long photoperiod (15L/9D). The effects of these treatments on gonadal weights are summarized in Figure 4.

At the beginning of treatment, testes and ovaries were in Stages 3 and III, respectively. In the July sample from nature, sacrificed with the experimentals, ovarian (Stage I) and testicular (Stage 0) regression was occurring. Testes and ovaries of fish at 27°C regressed as in nature; in both sexes gonad weights were significantly lower ($P < 0.01$) than initial levels.

In both groups at 13°C spermatogenetic activity remained at the initial levels and the testes did not show the regression seen in nature or at 27°C. Ovarian weights in the 13°C group at a long photoperiod were significantly lower ($P < 0.05$) than those of the initial May sample

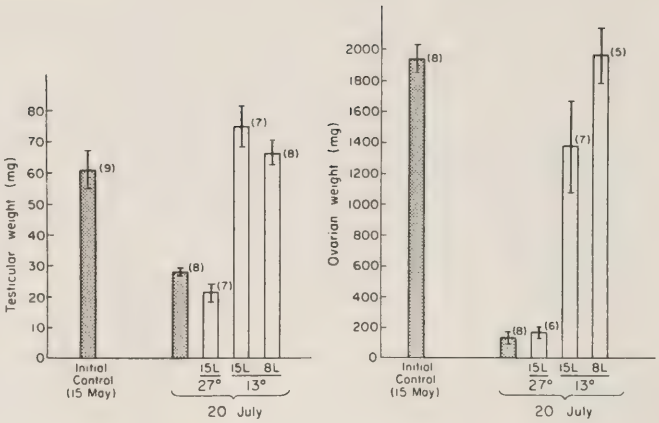

FIGURE 4.—Effect of 27° and 13°C treatments at short (8L/16D) and long (15L/9D) photoperiods on testicular and ovarian weight in *Gillichthys mirabilis*. Mean gonadal weight is represented by histograms; the mean is bracketed by one standard error. Shaded histograms represent gonadal weight of samples collected in nature; open histograms, experimental groups. Light (hours given per 24 hr), temperature, and dates on which fish were sacrificed are recorded below the histograms. Sample sizes are indicated atop each histogram.

and those of the 13°C group at a short photoperiod. Ovaries in both 13°C groups were, however, in active vitellogenesis (Stage III). These results could indicate a photoperiod influence in vitellogenesis. But one must observe caution in interpreting these data since this difference in ovarian condition may simply be a problem of beginning experiments with fish in various stages of oogenesis. Data presented by de Vlaming (1972b) revealed the nonsynchrony of gametogenesis in this species (i.e., fish in different stages of gonadal development were common in monthly samples between November and June).

High temperatures apparently cause testicular and ovarian regression in spring, at least when the photoperiod is long, whereas low temperatures prevent gonadal regression and are required for spermatogenesis and vitellogenesis.

EFFECTS OF CONSTANT TEMPERATURES AND PHOTOPERIOD ON FISH IN STAGES OF ACTIVE SPERMATOGENESIS (JANUARY)

In the previous experiment the influence of temperature and photoperiod was examined during the spawning season in spring. Whether fish respond similarly in winter (near the onset of the spawning season) is also of interest, so in January 1968 fish were exposed to 27°, 20°, and 13°C, at a short (8L/16D) or a long (15L/9D) photoperiod for 30-39 days. The influence of these treatments on testicular weight and histology is presented in Figures 5 and 6, respectively.

Testes of the initial January controls were in Stages 3, 4, or 5. As observed in May, testes regressed rapidly at 27°C; testes weights were significantly less ($P < 0.01$) than those of the January controls and February sample from nature. Histological examination confirmed that regression had occurred (testes in Stage 1). No photoperiod effect was seen at 27°C.

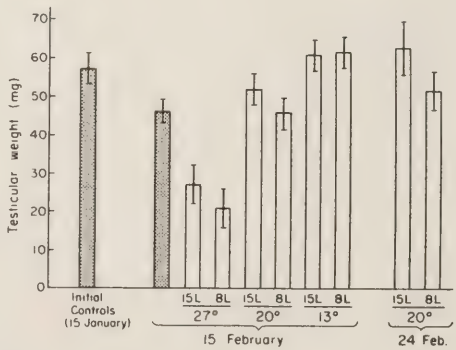

FIGURE 5.—Effect of 27°, 20°, and 13°C treatments at short (8L/16D) and long (15L/9D) photoperiods on testicular weight in *Gillichthys mirabilis*. Mean testicular weight is represented by histograms; the mean is bracketed by one standard error. Shaded histograms represent testicular weight of samples collected in nature; open histograms, experimental groups. Light (hours given per 24 hr), temperature, and dates on which fish were sacrificed are recorded below the histograms. For example sizes, see Figure 6.

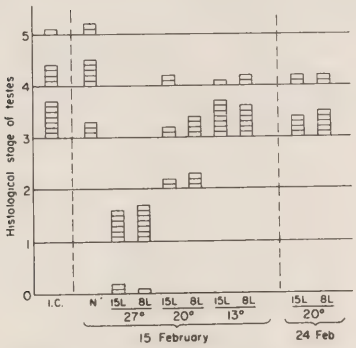

FIGURE 6.—Effect of 27°, 20°, and 13°C treatments at short (8L/16D) and long (15L/9D) photoperiods on testicular histology in *Gillichthys mirabilis*. I.C. refers to initial controls (15 January) and N, to sample from natural population. Each box represents the testicular condition of one fish.

Testicular weights in the 20°C groups remained at approximately the initial level. Both groups at 20°C had significantly heavier ($P < 0.01$) testes than those of the 27°C groups. The testes of all fish at 20°C advanced to Stages 3 or 4 by 24 February, and there was no clear photoperiod effect. Testicular weights of the 13°C groups did not differ significantly from the initial January controls but were significantly greater than those of the 20°C group at a short photoperiod ($P < 0.05$) and those of the 27°C groups ($P < 0.01$). Spermatogenic condition of the testes in the 13°C groups was essentially the same as in the January controls and February sample from nature (Figure 6).

The results of this experiment indicate that spermatogenesis is maintained at 13°C and 20°C (independent of photoperiod) but that this process may occur at a slower rate at 20°C than at 13°C. This difference in effect of these two temperatures must be accepted with some reservation because the variability of gonadal development in the initial controls could introduce a degree of bias into the results. Regardless of photoperiod, testicular regression occurred at 27°C.

EFFECTS OF HIGH TEMPERATURES ON GONADAL FUNCTION IN DIFFERENT SEASONS

Experiments using high temperatures were initiated at different times during the year to determine whether there is a seasonal variation in gonadal susceptibility to such treatment. The conditions employed and results obtained in these experiments are summarized in Table 3.

Experiments I and II indicate that 24°C is a sufficiently high temperature to initiate testicular regression within a relatively short period. With either a long (15L/9D) or a short (8L/16D) photoperiod (Experiment III), 25°C stimulates the completion of testicular regression within 21 days; testes of these fish were in the quiescent phase (Stage 1). A temperature

TABLE 3.—Effect of various high temperature and photoperiod treatments on testicular weight in *Gillichthys mirabilis*.

Experiment numbers	Date	Length of treatment (Days)	Temperature (°C)	Photoperiod (L/D)	Testicular weight (mg) ($\bar{x} \pm SE$)		
					Initial controls	After treatment	(n)
I	May 69	21	24	12/12	79.1 ± 5.2	58.1 ± 3.1**	(7)
II	Feb. 70	15	24	14/10	79.1 ± 9.5	34.4 ± 2.5**	(9)
III	Feb. 68	21	25	15/9	43.7 ± 3.4	25.0 ± 1.6*	(7)
	Feb. 68	21	25	8/16	43.7 ± 3.4	23.2 ± 4.8*	(7)
IV	July 70	30	27	10/14	22.3 ± 7.8	18.1 ± 1.4	(8)
V	Nov. 69	14	27	12/12	64.8 ± 8.8	30.0 ± 2.7**	(8)
VI	Apr. 70	8	27	12/12	97.8 ± 7.4	46.7 ± 3.9**	(10)
VII	July 68	41	24	12/12	33.1 ± 3.2	28.9 ± 2.2	(7)
	July 68	41	28	12/12	33.1 ± 3.2	18.1 ± 2.2*	(8)
VIII	June 68	21	27	12/12	52.2 ± 3.9	26.2 ± 2.7**	(7)
	June 68	21	30	12/12	52.2 ± 3.9	14.8 ± 3.1**	(8)
IX	Apr. 68	8	28	12/12	62.2 ± 5.4	40.1 ± 4.2**	(7)
	Apr. 68	14	28	12/12	62.2 ± 5.4	24.3 ± 1.8**	(9)
	Apr. 68	8	32	12/12	62.2 ± 5.4	15.6 ± 2.8**	(8)

*Significantly less ($P < 0.05$) than initial controls.
**Significantly less ($P < 0.01$) than initial controls.

of 25°C does not, however, block mitotic proliferation of spermatogonia.

Experiment IV (Table 3) indicates that 27°C blocks the initiation of testicular recrudescence. Testicular regression is initiated within 14 days at 27°C (Experiment V); the testes of all fish were in the regression phase (Stage 0). Moreover, Experiment VI suggests that testicular regression is initiated within 8 days at 27°C; the testes of all fish were regressing (Stage 0).

When initial controls are undergoing testicular regression, 28°C stimulates a more rapid completion of regression than does 24°C (Experiment VII). This is evident since the testes of a majority of the fish at 28°C were in the quiescent phase (Stage 1) whereas those of the 24°C group were in Stage 0. A 30°C temperature (Experiment VIII) causes a more complete testicular regression than does a 24°C temperature (i.e., testicular weights of the 30°C group were significantly lower ($P < 0.01$) than those of the 27°C group). Both of these treatments caused the completion of testicular regression within 21 days; the testes of a majority of fish in both groups were in the quiescent phase (Stage 1). Similarly, 32°C stimulates a more rapid and more complete testicular regression than 28°C (Experiment IX); testicular weights after 8 days were significantly lower ($P < 0.01$) in the 32°C group than those of the 28°C group. Testes of all fish at both temperatures were regressing (Stage 0). After 14 days at 28°C, testicular weights were still significantly higher ($P < 0.05$) than testicular weights after 8 days at 32°C (Experiment IX).

With the exception of the experiments in which the initial controls were fish with regressing gonads, all high temperature treatments summarized in Table 3 caused a significant decrease in testicular weights. These data indicate that the rate of testicular regression and the degree of testicular regression are temperature dependent. These data also indicate that under laboratory conditions testicular involution is initiated relatively soon after exposure to high temperatures and that regression can be completed rapidly in this species.

Experiments similar to those discussed above were conducted with female *Gillichthys* (Table 4). Beginning with fish in active vitellogenesis (Stage III), 25°C initiates ovarian regression (Stage I) within 21 days, independent of photoperiod (Experiment 1). Ovarian weights in the two photoperiod groups were not significantly different. Beginning with fish having regressing ovaries (Experiment 2), 27°C caused the completion of ovarian regression. Experiment 3 suggests that ovarian regression is complete within 21 days at 30°C; the ovaries of a majority of the initial controls were in phases of active vitellogenesis (Stage III), whereas following treatment, the ovaries of all fish were in the quiescent phase (Stage II).

Experiment 4 (Table 4) indicates that 32°C stimulates a more rapid rate of ovarian regression than does 28°C; ovarian weights of the 32° and 28°C groups were significantly different ($P < 0.01$) after 8 days of treatment. Ovarian regression was occurring in all fish. After 14 days at 28°C, further ovarian regression occurred, but involution had still not been completed.

Therefore, temperatures between 25° and 32°C initiate ovarian regression within a relatively short time; all high temperature treatments caused a significant decrease in ovarian weights. Apparently the completion of ovarian regression is temperature dependent.

EFFECTS OF 21°-22°C AND PHOTOPERIOD TREATMENT ON GONADAL FUNCTION

The previous experiments suggest that gonadal regression occurs at 24°C but not at 20°C. To define more precisely the thermal threshold for gonadal involution, the effects of 21°-22°C treatments were examined in April, May, September, and November. The conditions employed and results obtained in these experiments are summarized in Table 5.

Beginning in April with fish in active spermatogenesis or in the prespawning condition (Stage 3 or 4), there was no change in testes after 17-day treatment at 22°C (15L/9D). However, after 30-day treatment at 22°C and a short photoperiod (10L/14D), there was a significant decrease ($P < 0.01$) in both ovarian and testicular weights (Experiment 11—Table 5). Testes

TABLE 4.—Effect of various high temperature and photoperiod treatments on ovarian weight in *Gillichthys mirabilis*.

Experiment number	Length of treatment (Days)	Temperature (°C)	Photoperiod	Weight of ovaries (mg) ($\bar{x} \pm$ SE)		
				Initial controls	After treatment	(n)
1	21	25	15L/9D	1,744 ± 422	381 ± 81**	(7)
	21	25	8L/16D	1,744 ± 422	480 ± 108**	(8)
2	30	27	10L/14D	484 ± 98	188 ± 4*	(8)
3	21	30	12L/12D	1,638 ± 219	190 ± 76**	(8)
4	14	28	12L/12D	3,042 ± 305	654 ± 181**	(6)
	8	28	12L/12D	3,042 ± 305	1,790 ± 423**	(6)
	8	32	12L/12D	3,042 ± 305	871 ± 312**	(8)

*Significantly less ($P < 0.05$) than initial controls.
**Significantly less ($P < 0.01$) than initial controls.

of the May controls were in active spermatogenesis (Stage 3) or in the prespawning conditions (Stage 4); ovaries of the May controls were in active vitellogenesis (Stage III). The testes of six of the eight fish at the short photoperiod, however, were regressing (Stage 0); ovaries in this group were regressing (Stage I) or in the quiescent phase (Stage II).

In contrast to the effects of short photoperiod at 22°C, a long photoperiod (in May) did not initiate testicular regression. Although testicular weights in this group were significantly less ($P < 0.05$) than those of the initial May controls, the testes of all fish were in active spermatogenesis (Stage 3). Ovarian weights of fish at a long photoperiod were also significantly lower ($P < 0.01$) than those of the initial May controls; ovarian regression (Stage I) was occurring in all fish.

Beginning in September, 26-day exposure to a short photoperiod (10L/14D) at 21°C stimulated a significant increase ($P < 0.05$) in ovarian and testicular weights when compared to gonadal weights in the initial controls (Experiment 12—Table 5). In contrast, neither ovarian nor testicular weights in the long photoperiod group were significantly altered. The testes of the September controls were in Stage 2, and the ovaries of this group were in early stages of vitellogenesis (Stage III). After short photoperiod treatment, the gonads of all fish were in the meiotic phase of spermatogenesis (Stage 3) or vitellogenesis (Stage III); the long photoperiod, however, did not stimulate spermatogenesis (testes in this group were in Stage 1) and caused ovarian regression (Stage I).

Beginning in November (Experiment 13), testicular weights were maintained at the initial level for 21 days at 22°C and a short photoperiod (10L/14D); testes of the initial controls and the experimental fish were in Stage 3 or 4. A long photoperiod at 22°C, however, caused the initiation of testicular regression (Stage 0); testicular weights in this group were significantly

TABLE 5.—Effect of 21° and 22°C treatments on testicular and ovarian weight in *Gillichthys mirabilis*.

Experiment number	Beginning date	Length of treatment (Days)	Temperature (°C)	Photoperiod		Gonadal weight (mg) ($\bar{x} \pm$ SE)		
						Initial controls	After treatment	(n)
10	April	17	22	15L/9D	males:	97.8 ± 7.4	99.2 ± 8.8	(10)
11	May	30	22	10L/14D	males:	88.4 ± 7.1	43.3 ± 2.3**	(8)
					females:	1,283 ± 186	681 ± 242**	(7)
11	May	30	22	15L/9D	males:	88.4 ± 7.1	70.6 ± 6.1*	(8)
					females:	1,283 ± 186	631 ± 216**	(6)
12	September	26	21	10L/14D	males:	42.8 ± 7.4	61.5 ± 7.8*	(8)
					females:	233 ± 39	364 ± 44*	(6)
12	September	26	21	15L/9D	males:	42.8 ± 7.4	36.0 ± 4.2	(7)
					females:	233 ± 39	166 ± 21	(6)
13	November	21	22	15L/9D	males:	68.5 ± 9.7	46.9 ± 6.3**	(10)
13	November	21	22	10L/14D	males:	68.5 ± 9.7	79.5 ± 5.1	(8)

*Significantly different ($P < 0.05$) from initial controls.
**Significantly different ($P < 0.01$) from initial controls.

lower ($P < 0.01$) than those of the initial November controls.

In spring spermatogenesis occurs at 22°C only if the photoperiod is long and in autumn only if the photoperiod is short. This temperature causes ovarian regression regardless of photoperiod, suggesting that females may be more sensitive to temperature than males. Similarly, 21°C will promote the initiation of testicular and ovarian recrudescence only if photoperiod is short. Apparently then, the effects of photoperiod at these temperatures are seasonally variable.

EFFECTS OF PHOTOPERIOD AT 20°C ON FISH WITH REGRESSING OR QUIESCENT GONADS

Experiments reported above showed that gonadal recrudescence will not occur at 20°C if treatment is initiated in July but that gametogenesis is maintained at this temperature at other times during the year. Thus, the influence of 36-day 20°C treatment at various photoperiods on gonadal recrudescence was examined in August 1968 (Figure 7). The gonads of the initial August controls were in Stages 0 and 1. Neither testicular nor ovarian weights in any of the experimental groups varied significantly from gonadal weights in the initial August controls, and there were no significant differences in gonadal weights among the experimental groups. Differences in gonadal histology were, nonetheless, evident. Testes of all fish collected from nature in August and September were in the regression phase (Stage 0). In all photoperiod groups testicular regression was complete, and spermatogonial proliferation (Stage 2) or spermatogenesis (Stage 3) was occurring. The testes of 4 of 10 fish at a 15L/9D photoperiod, however, were in the quiescent phase (Stage 1). A majority of ovaries from fish collected from nature in August and September were in the quiescent phase (Stage II). In each experimental group, the ovaries of some fish were in the early phases of vitellogenesis (Stage III); with the exception of one fish, vitellogenesis was initiated in all females at 15L/9D.

These results indicate that gonadal recrudescence is initiated at 20°C if treatment is begun

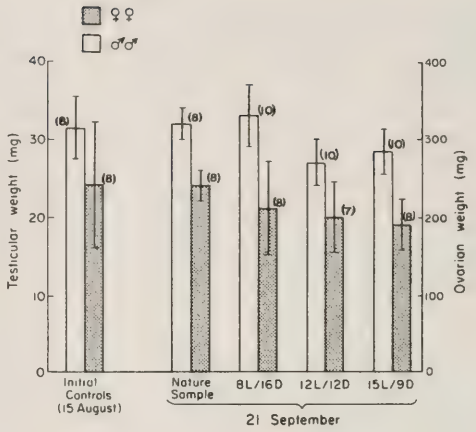

FIGURE 7.—Effect of 36-day 20°C treatment at various photoperiods on ovarian and testicular weight in *Gillichthys mirabilis*. Shaded histograms illustrate mean ovarian weights; open histograms illustrate mean testicular weights; the means are bracketed by one standard error. Photoperiod treatments are given below the histograms. Sample sizes are indicated atop each histogram.

in August. Recrudescence was initiated after 36 days in all photoperiod groups, but a long photoperiod (15L/9D) was most effective in females and least effective in males.

EFFECTS OF 16°C TREATMENT ON GONADAL FUNCTION

Gonadal recrudescence does not normally occur if *Gillichthys* is exposed to 20°C in July. To examine whether recrudescence could be initiated in July at a slightly lower temperature, the effect of 16°C treatment was determined. Before examining the effects of this temperature treatment on recrudescence, an experiment was conducted in January to be certain that gametogenesis could be maintained at this temperature. The ovaries of the initial January controls (Table 6) were in Stage III, IV, or V; the testes of fish in this sample were in Stage 4 or 5. Neither testicular nor ovarian weights were significantly altered by this 90-day treatment, nor was there an evident change in gonadal activity as judged by histological examination.

The testes and ovaries of the initial controls of the July experiment (Table 6) were regres-

sing (Stages 0 and I). Following 80-day treatment at 16°C, ovarian and testicular weights were significantly greater ($P < 0.01$) than those of the initial controls. Testes of the experimental fish were in Stage 3 or 5. Ovaries of fish in the 16°C group were in Stage II or III.

The results of these experiments indicate that spermatogenesis and vitellogenesis are maintained at 16°C. In fish with regressing gonads (collected in July), 16°C treatment initiates spermatogenesis and oogenesis.

EFFECTS OF LONG PHOTOPERIOD TREATMENT (15°C) ON FISH WITH REGRESSING TESTES

In July 1969 an experiment was initiated to determine whether a long photoperiod could block recrudescence at an "intermediate" temperature. All of the initial controls were undergoing testicular regression (Stage 0); the mean (± SE) testicular weight (mg) in this sample was 32.3 ± 2.2. Fish were exposed to 15°C for 30 days at a 15L/9D photoperiod. At the termination of the experiment a sample of fish was taken from nature; the mean testicular weight (± SE) in this group was 20.7 ± 3.2, and the testes of these fish were regressing (Stage 0). Testicular weights ($\bar{x} \pm SE = 58.3 \pm 7.3$) of the 15°C group were significantly greater ($P < 0.01$) than those of the initial July controls and the September sample from nature. The testes of nine fish in the 15°C group were in Stage 3, and those of three were in Stage 4. These data suggest that 15°C treatment initiates testicular recrudescence, even when the photoperiod is long.

TABLE 6.—Effect of 16°C treatment (12L/12D) on testicular and ovarian weight in *Gillichthys mirabilis*.

Beginning date	Length treatment (Days)	Sex	Gonadal weight (mg) ($\bar{x} \pm SE$)		
			Initial controls	After treatment	(n)
January	90	Males	71.6 ± 4.9	66.7 ± 4.0	(10)
		Females	1,321 ± 295	1,136 ± 238	(11)
July	80	Males	32.3 ± 2.2	54.5 ± 4.1**	(10)
		Females	256 ± 23	438 ± 34**	(10)

**Significantly greater ($P < 0.01$) than initial controls.

EFFECTS OF 12° AND 20°C TREATMENT ON FISH IN STAGES OF ACTIVE GAMETOGENESIS

Data presented above suggest that gametogenesis may be maintained more effectively at 13°C than at 20°C. Beginning in March 1968, fish were exposed to 20° and 12°C for 21 days to examine this possibility (Table 7). The ovaries of the initial March controls were in phases of active vitellogenesis (Stage III) or the prespawning or postspawning condition (Stage IV or V); the testes of this group were in Stage 3.

TABLE 7.—Effect of 21-day 12° and 20°C treatments on ovarian and testicular weights in *Gillichthys mirabilis*.

Experimental group	Gonadal weight (mg) ($\bar{x} \pm SE$)			
	Males	(n)	Females	(n)
Initial controls (March)	59.3 ± 6.1	(11)	1,038 ± 198	(11)
12°C treatment	74.7 ± 6.3*	(10)	1,428 ± 106	(8)
20°C treatment	58.8 ± 5.7	(7)	1,375 ± 123	(8)
Terminal controls (April)	62.2 ± 5.4	(8)	3,043 ± 297	(18)

*Significantly greater ($P < 0.05$) than initial controls.

Ovarian weights in the two experimental groups did not differ significantly from those of the initial March controls, but they were significantly less ($P < 0.01$) than ovarian weights of the sample taken from nature at the time of sacrifice (April). Ovaries of the 20° and 12°C groups were in Stage III or IV; the ovaries of a majority of the April sample from nature were in Stage IV.

Testicular weights in the 20°C group were not significantly altered by treatment, but those of the 12°C group were significantly greater ($P < 0.05$) than the testicular weights of the initial March controls. The testes of fish in the 12°C group were in Stage 3 or 4; however, the testes of four of seven fish at 20°C were in Stage 2 and the remainder in Stage 3.

These data indicate that at a 12L/12D photoperiod, vitellogenesis and spermatogenesis will occur at both 12° and 20°C but that the lower temperature is more effective. Neither of these treatments, however, was as effective in promoting vitellogenesis as the factors acting on the natural population.

INHIBITION OF TESTICULAR REGRESSION BY LOW TEMPERATURE

An experiment was initiated in June 1968 to resolve whether low temperature treatment in combination with a short photoperiod could prevent gonadal regression at the "normal" time (early July). The testes of the beginning controls were in the prespawning or postspawning conditions (Stages 4 or 5). Fish were exposed to 10° or 20°C at a 10L/14D photoperiod for 21 days. The testes of fish collected from nature at the time of sacrifice (July) of the experimentals were regressing (Stage 0). Testicular weights in the 10°C group ($\bar{x} \pm SE = 60.7 \pm 4.1$) and the 20°C group ($61.0 \pm 6.2$) did not vary significantly from those (52.2 ± 3.9) in the initial June controls, but those of both groups were significantly greater ($P < 0.01$) than testicular weights of the July sample from nature (32.1 ± 3.1). The testes of 10 fish exposed to 10°C and 6 fish to 20°C were in active spermatogenesis (Stage 3), and 4 in each group were in the prespawning condition (Stage 4). Thus, testicular regression does not occur at the normal time when fish are exposed to temperatures between 10° and 20°C.

COMPARATIVE EFFECTS OF 10° AND 18°C TREATMENT ON GONADAL RECRUDESCENCE

To determine whether there is a differential effect of 10° and 18°C on gonadal recrudescence, a 21-day experiment was initiated in August 1970 with fish having regressing or quiescent gonads (Stages 0 and 1). The effects of these treatments on gonadal weight are presented in Table 8.

TABLE 8.—Effect of 21-day 10° and 18°C treatments (13L/11D) on ovarian and testicular weights in *Gillichthys mirabilis*.

Experimental group	Gonadal weight (mg) ($\bar{x} \pm SE$)			
	Males	(n)	Females	(n)
Initial controls (August)	32.5 ± 2.1	(10)	280 ± 18	(8)
10°C treatment	42.6 ± 4.4*	(8)	339 ± 48	(8)
18°C treatment	41.7 ± 7.3*	(8)	386 ± 33*	(8)

*Significantly greater ($P < 0.05$) than initial controls.

A significant increase ($P < 0.05$) in testicular weights occurred at both 10° and 18°C; testicular weights in the two groups were not significantly different. Spermatogenesis was initiated in all fish in both experimental groups. Ovarian weights in fish exposed to 18°C were significantly greater ($P < 0.05$) than those of the initial August controls; however, ovarian weights in the 10°C group were not significantly different than those of the initial controls or those of the 18°C group. Nonetheless, the ovaries of all fish in both experimental groups were in early phases of vitellogenesis (Stage III).

These data indicate that there is little or no difference in the rate of initiation of gonadal recrudescence at 10° and 18°C. The possibility exists, however, that following the initiation of recrudescence, the rate of testicular and ovarian growth could be different at the two temperatures.

DISCUSSION

In previous work (Barlow and de Vlaming, 1972; de Vlaming, 1972b), the gonadal cycle of *Gillichthys* was observed to be closely correlated with seasonal changes in several environmental variables. Gonadal regression occurs as daylength begins to shorten and temperature reaches a seasonal maximum. The initiation of gonadal recrudescence coincides with the decline in temperature and the continued decrease in daylength. A majority of the spawning in this species occurs when daylength and temperature are increasing. The data presented here suggest that temperature may be important with regard to reproductive cycling, photoperiod acting only to modify the responses to temperature.

GONADAL REGRESSION

In these laboratory experiments, constant temperatures of 24°C and above cause testicular and ovarian regression at any time of the year regardless of photoperiod (i.e., photoperiod does not seem to have an influence on gonadal regression). As temperature is increased above 24°C, shorter treatment periods are required to attain the ovarian and testicular quiescent phases.

High temperatures bring about ovarian regression by inhibiting vitellogenesis and causing atresia of all yolky oocytes. In males, high temperatures apparently increase the rate of meiotic divisions and the process of spermiogenesis; this is apparent because the testes of fish sacrificed soon after the initiation of high temperature treatment are characterized by large numbers of secondary spermatocytes and spermatids. Fish sacrificed after longer treatments at high temperatures, however, are characterized by testes with only primary spermatogonia, suggesting that high temperatures inhibit the transformation of spermatogonia into primary spermatocytes. High temperatures also cause the "flaking off" of cysts of spermatocytes from the germinal epithelium into the lumen of the testicular lobules. Moreover, pyknotic degeneration of spermatocytes, spermatids, and spermatozoa occurs at high temperatures, followed by phagocytosis of cellular debris. Mitotic proliferation of spermatogonia is inhibited above 25°C, but treatment at 27°C for 15 days does not inactivate the sperm remaining in the testes. Weisel (1948) showed that the spermatozoa of *Gillichthys* remain alive in vitro for 2 weeks at 2°-4°C, but at 24°-26°C they are immobile in 33 hr.

In *Gillichthys* the termination of the reproductive season is apparently not endogenously timed. Regression is not "obligatory" since low temperature treatments (regardless of photoperiod) prevented gonadal involution at the "normal" time (July). These studies imply that the reproductive cycle of this species is primarily under exogenous regulation. A similar situation has been reported in the cyprinodontid, *Epiplatys bifasciatus* which occurs in the Zio River and Lagoon of Lomé of the Republic of Togo, Africa (Loiselle, 1969). *Gillichthys* is thus apparently a potentially continuous breeder but has a reproductive cycle imposed upon it by the increased temperatures of summer. Although little information is available on the causes of termination of reproductive cycles, differences are evident. For example, Baggerman (1957) suggested that since none of the experimental conditions she tested could maintain continuous breeding in *Gasterosteus aculeatus*, termination of the cycle is endogenously controlled. The rate of postspermatogonial regression is also accelerated by warm temperatures, and low temperatures retard the rate of sexual regression in *Fundulus heteroclitus* (Lofts, Pickford, and Atz, 1968).

GONADAL RECRUDESCENCE

In *Gillichthys* gonadal recrudescence does not occur at constant temperatures of 24°C or above, regardless of photoperiod. Long-term experiments indicate that gonadal recrudescence is not initiated in males or females after nearly 4 months at high temperatures (comparable to summer temperatures). High temperatures also retard the early phases or intermediate phases of gametogenesis in *Fundulus heteroclitus* (Burger, 1939), *Phoxinus laevis* (Bullough, 1939), female *Apeltes quadracus* (Merriman and Schedl, 1941), *Enneacanthus obesus* (Harrington, 1956), female *Fundulus confluentus* (Harrington, 1959), *Couesius plumbeus* (Ahsan, 1966), and *Cymatogaster aggregata* (Wiebe, 1968).

Experiments, begun in winter and spring with the longjaw goby in phases of active gametogenesis, indicate that gonadal activity is maintained at 20°C over a wide range of photoperiods; long photoperiods may be more effective in this regard, but more experiments are needed to prove conclusively the influence of photoperiod. Beginning in July with fish having regressing testes, mitotic proliferation of spermatogonia was stimulated, especially with a short photoperiod, but complete recrudescence did not occur at 20°C. However, beginning in August with fish having regressing testes, recrudescence did occur at 20°C; a short photoperiod was more effective in this respect. Beginning in September, testicular and ovarian recrudescence is initiated at 21°C, but only with a short photoperiod. The rate of spermatogenesis was, however, extremely low at these temperatures. Thus, a shift in gonadal responsiveness to 20°C apparently occurs between July and August. The experiment beginning in July was continued for 3 months without the initiation of spermatogenesis whereas the experiment beginning in August was terminated after a much shorter time. The

adaptive significance of the "refractoriness" to 20°C in July may be to prevent "premature" initiation of spermatogenesis should temperatures decrease somewhat during the regression phase.

Although the data presented here are by no means conclusive, they suggest that photoperiod has a variable effect at 20°C. Long photoperiods may be more effective in maintaining spermatogenesis whereas short photoperiods seem to promote a faster rate of recrudescence at 20°C. Moreover, active spermatogenesis is maintained at 22°C only with a long photoperiod. Differences are evident between the sexes since vitellogenesis does not occur at this temperature regardless of photoperiod. Since a majority of spawning in *Gillichthys* occurs when daylength is increasing and recrudescence occurs when daylength is decreasing, the variation in the effects of photoperiod seen here seem reasonable.

That 20°C is not as effective as lower temperatures in maintaining gametogenesis or promoting gonadal recrudescence is consistent with the phenological and climatic data presented by de Vlaming (1972b). Average daily temperatures are below 20°C from early October to mid-June; it is during this period that most of the gonadal activity occurs in this species.

Complete gonadal recrudescence in both male and female *Gillichthys* occurred at 12° and 13°C, suggesting that the decreasing temperatures in autumn are primarily responsible for regulating this process. Constant low temperature treatment promoted a faster rate of recrudescence than occurred in the natural population. Diurnal increases in temperature in the natural habitat during autumn may account for the slower rate of gonadal recrudescence. Short photoperiods augmented the rate of recrudescence at low temperatures in both males and females. Thus, the decreasing photoperiod in autumn probably facilitates, but is not essential for, the effects of decreasing environmental temperatures in promoting gonadal recrudescence.

With a 12L/12D photoperiod, gonadal recrudescence was initiated within 21 days at 10° and 18°C. This suggests that gonadal response in this species is relatively fast; rapid mobilization of energy for gonadal recrudescence may be characteristic of species that spawn more than once in a season. Whether recrudescence was more rapid at 10° or 18°C was not investigated, nor are there sufficient data to indicate whether an optimal temperature exists for the completion of gonadal recrudescence. However, the data presented here show that gonadal recrudescence will occur over a wide temperature range (10°-20°C). This gonadal responsiveness to a wide range of temperatures may reflect an adaptation to the labile thermal environment of this species.

Active gametogenesis was maintained at low temperatures regardless of photoperiod. After treatment at a low temperature in May (Figure 4), more male fish were in the prespawning condition at the longer photoperiod. In the same experiment, however, a short photoperiod was more effective in maintaining vitellogenesis (Figure 4). Perhaps these results reflect a true photoperiod influence, but because of the variable gonadal conditions of the beginning controls no conclusive statements can be advanced. In fact, experiments begun in January with fish revealing less variable gonadal conditions indicated that long and short photoperiod treatments maintained active gametogenesis equally well at low temperature. Photoperiod influences, however, could vary between January and May.

The question arises as to why all fish treated at low temperatures did not progress to the prespawning condition. One possible explanation is that many of the experiments discussed here were relatively short term. In many of the long-term experiments some of the fish could be stripped of ripe eggs and sperm. It is likely, however, that physical factors other than temperature and photoperiod, and also social factors, influence final gonadal maturation and spawning in this species. Indeed, Weisel (1947) has indicated that *Gillichthys* is territorial and has an elaborate courtship behavior. In addition, de Vlaming (1971b) has shown that salinity changes and changes in the availability of food can alter the rate of gametogenesis in *Gillichthys*. Thus, the failure of many of the experimental fish to completely attain the prespawning condition was probably due to the absence of certain conditions in the laboratory sit-

uation. Unfortunately, no data are available on the effects of exogenous factors on the frequency of spawning, fecundity, egg size, or survivorship of the fry in this species, nor are data available on the influence of environmental factors on the spawning act. For a complete understanding of the role of the environment in the physiology and ecology of reproduction in *Gillichthys*, examination of these parameters is needed.

The data presented here indicate that temperature may be the proximate factor regulating the *Gillichthys* reproductive cycle. Zambrano (1971) found that the secretory activity of the pituitary gonadotrophic cells is altered by temperatures, and this provides further support for this suggestion. However, since fish in their natural habitat experience large diurnal temperature fluctuations, the experiments reported here are not conclusive. In addition, *Gillichthys* is capable of regulating its body temperature by behavioral means (de Vlaming, 1971a). These experiments do set the physiological limits with regard to the influence of temperature on reproduction. Understanding the ecological meaning of temperature in reproductive cycling requires experimentation with diurnally fluctuating temperature; experiments of this nature are reported elsewhere (de Vlaming, 1972c).

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KINDS AND ABUNDANCE OF FISH LARVAE IN THE EASTERN TROPICAL PACIFIC ON THE SECOND MULTIVESSEL EASTROPAC SURVEY, AND OBSERVATIONS ON THE ANNUAL CYCLE OF LARVAL ABUNDANCE

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ABSTRACT

This is the second and concluding paper dealing with kinds and abundance of fish larvae in the eastern tropical Pacific based on collections made on EASTROPAC survey cruises. Main emphasis is placed on the composition and abundance of fish larvae on the second multivessel EASTROPAC cruise, occupied by three research vessels during August-September 1967. This cruise, spaced 6 months after EASTROPAC I, affords interesting comparisons of composition and relative abundance of fish larvae during two contrasting periods of the year. Counts of fish larvae per haul on EASTROPAC II were about 50% greater than on EASTROPAC I; species composition, however, was strikingly similar in the two surveys.

A portion of the EASTROPAC pattern, lying between long 119° to 98°W and lat 20°N to 3°S, was covered on four additional monitoring cruises—providing coverage of this more restricted area on six cruises, spaced at 2-month intervals, between February 1967 and January 1968. Essentially the same kinds of fish larvae were taken on each of the six coverages of the monitoring pattern, and for most species the range in relative abundance during the annual cycle was 3× or less.

This report deals with the composition and relative abundance of fish larvae in the eastern tropical Pacific Ocean collected on the second multivessel survey cruise made as part of EASTROPAC, during August-September 1967. For brevity, the cruise is referred to in this report as EASTROPAC II (ETP II). This cruise, conducted 6 months after EASTROPAC I (ETP I), deals with the composition of fish larvae at a contrasting period of the annual spawning cycle in tropical waters (Ahlstrom, 1971).

Three research vessels participated in ETP II: *Washington* operated by the Scripps Institution of Oceanography occupied the outer pattern, *Undaunted* of the National Marine Fisheries Service occupied the middle pattern, and *Rockaway* operated by the Coast Guard took the inner pattern (Figure 1).

The coverage during ETP II was less extensive than that of the four vessels of ETP I. One major line of stations of ETP I was omitted from ETP II, that along long 126°W, and the coverage below the equator was abbreviated in the two outer patterns, with lines ending at lat 10°S or 5°S.

Comparison of the composition, relative abundance, and distributions of fish larvae at different periods of the year in tropical waters is a primary objective of this report. The major comparison is with fish larvae obtained on ETP I (Ahlstrom, 1971); all of the 355 ETP II collections and an equivalent number of ETP I collections can be used to show similarities and differences in the composition of the larval fish fauna during two contrasting periods of the year.

A portion of the EASTROPAC pattern was occupied by the National Marine Fisheries Service research vessel, *David Starr Jordan*, on

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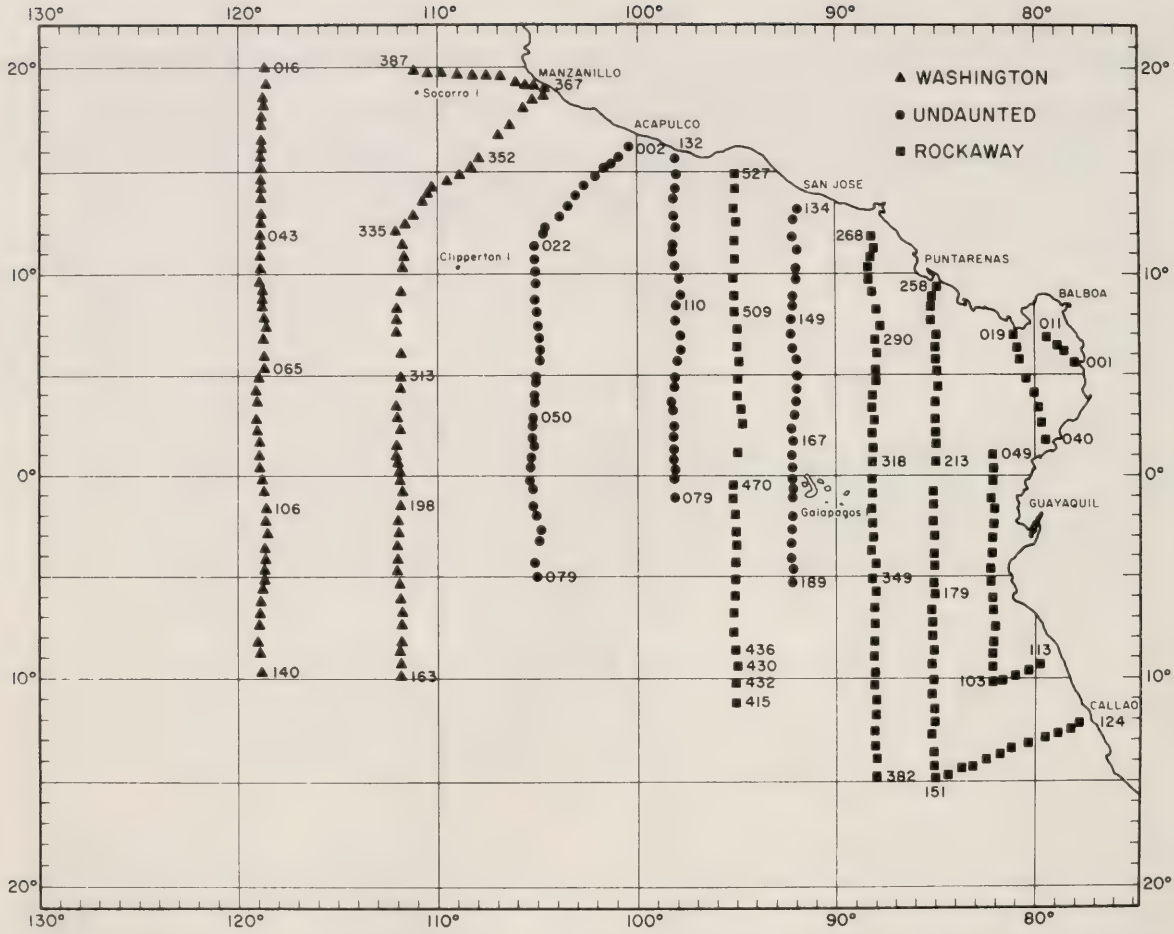

FIGURE 1.—Location of plankton stations occupied by three research vessels participating in the second multivessel EASTROPAC survey (ETP II). Symbols for vessels indicated in legend above. Samples collected by *Washington* are numbered as 45.000 series (for example 45.016, 45.140, 45.387), samples from *Undaunted* as 46.000 series, from *Rockaway* as 47.000 series.

monitoring cruises, spaced at bimonthly intervals between the multivessel cruises; coverages equivalent to the monitoring pattern were summarized for ETP I and ETP II, in order to compare the results of six bimonthly coverages of the same area (Figure 2). The monitoring pattern lacked coverage in the nearshore portion of the EASTROPAC pattern that was occupied by the inner vessel on multivessel surveys. Additional seasonal information about composition and relative abundance of fish larvae in this area was supplied by a "zig-transect" of 50 stations occupied by the RV *Oceanographer* of the Environmental Science Services Administration during November 1967—2 to 3 months after ETP II coverage of this area (Figure 2).

The methods of making zooplankton hauls on ETP II were identical to those previously described for ETP I (Ahlstrom, 1971). This paper deals solely with collections obtained from oblique hauls made with a net, 1-m mouth diameter, constructed of 505 μ nylon (Nitex) cloth, with approximately a 5:1 ratio of effective straining surface, i.e., pore area to mouth area.

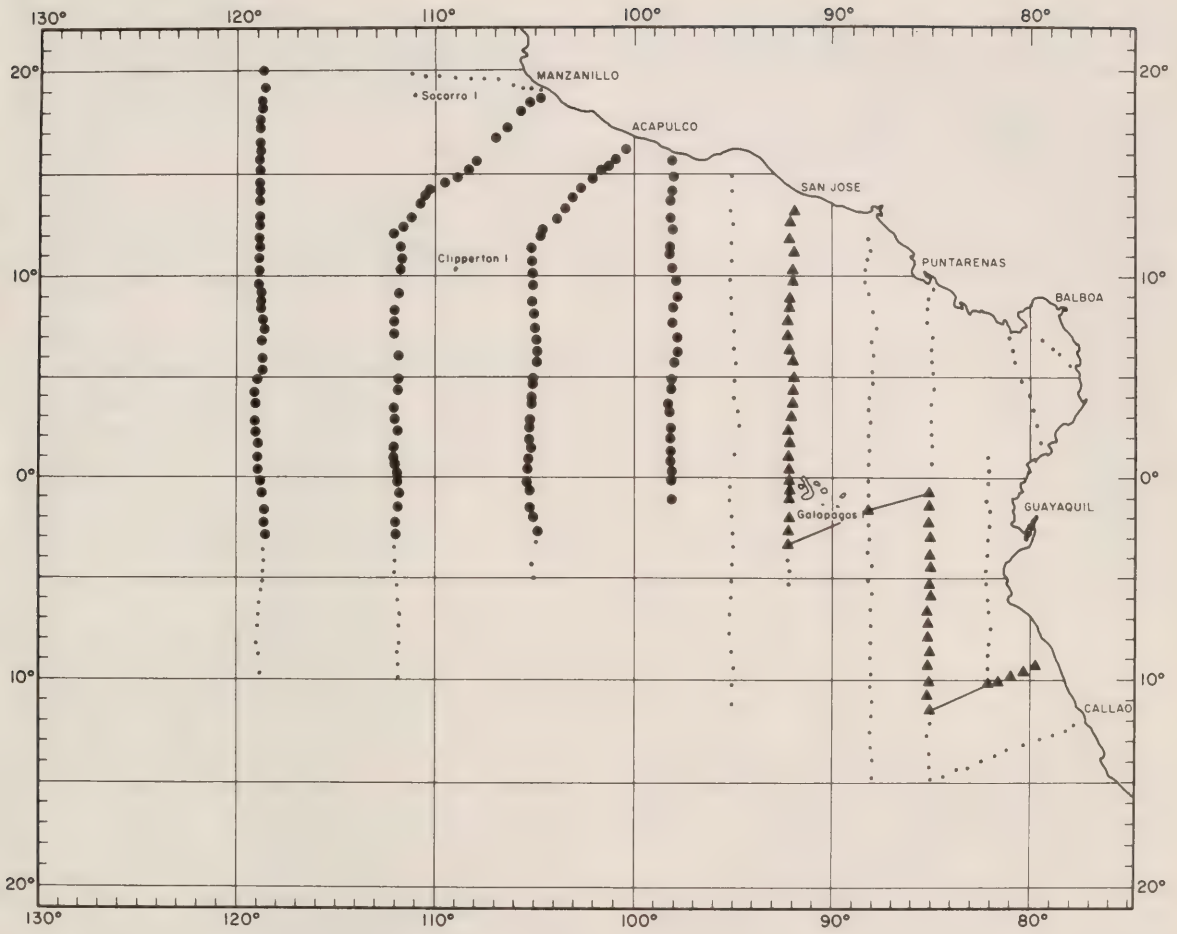

FIGURE 2.—Location of monitoring pattern (large solid circles), occupied between multivessel EASTROPAC cruises at 2-month intervals by *David Starr Jordan*, and of zig-transect pattern (triangles) occupied by *Oceanographer* during November 1967, superimposed on ETP II pattern.

As on ETP I, this net was paired in an assembly frame with a finer-meshed 0.5-m net. Each tow attempted to obtain a uniform sampling of zooplankton in the water column between the surface and approximately 200-m depth. The net assembly was lowered to depth by paying out 300 m of towing cable and then retrieved at a uniform rate. The depth reached by the net was estimated from the angle of stray (departure from the vertical) of the towing cable. The average depths of haul taken by the three research vessels are summarized in Table 1. Only slightly over two-thirds of the hauls were lowered to depths of 200 m or more and about one-eighth were taken at depths shallower than 180 m. Based on variation in depths sampled, speed of hauling was controlled less consistently on ETP II as compared with ETP I.

Four plankton collections were made each day with the paired net-assembly, at about 6-hr intervals. Timing of hauls was not coordinated between research vessels (Table 2). Usually *Rockaway* spaced the four hauls at approximately 0500, 1030, 1700, and 2300; hauls from *Wash-*

TABLE 1.—Depths of paired oblique pankton hauls taken by the three research vessels in EASTROPAC II (net lowered by paying out 300 m of towing cable).

Average depth of haul (m)	Number of hauls taken at each depth interval from			
	Washington 45.000 Series	*Undaunted* 46.000 series	*Rockaway* 47.000 Series	All vessels
80.1- 90.0	--	1	--	1
90.1-100.0	--	--	--	--
100.1-110.0	--	--	--	--
110.1-120.0	--	1	--	1
120.1-130.0	--	2	--	2
130.1-140.0	1	--	--	1
140.1-150.0	1	--	3	4
150.1-160.0	2	4	1	7
160.1-170.0	--	5	4	9
170.1-180.0	7	4	6	17
180.1-190.0	6	4	3	13
190.1-200.0	24	16	14	54
200.1-210.0	36	22	52	110
210.1-220.0	28	28	56	112
220.1-230.0	5	6	7	18
230.1-240.0	1	--	1	2
240.1-250.0	--	--	1	1
250.1-260.0	--	--	1	1
260.1-270.0	--	2	--	2
Total	111	95	149	355

TABLE 2.—Hour of day that paired oblique plankton hauls were made from the three research vessels participating in EASTROPAC II (midtime of haul used).

Hour of day	Number of hauls taken during each hour of the day			
	Washington	*Undaunted*	*Rockaway*	All vessels
0001-0100	10	10	8	28
0101-0200	4	0	1	5
0201-0300	1	0	3	4
0301-0400	0	1	3	4
0401-0500	0	10	14	24
0501-0600	5	8	15	28
0601-0700	12	3	4	19
0701-0800	5	1	0	6
0801-0900	2	0	1	3
0901-1000	1	0	6	7
1001-1100	1	0	21	22
1101-1200	10	14	6	30
1201-1300	11	11	1	23
1301-1400	3	0	1	4
1401-1500	3	0	2	5
1501-1600	2	0	12	14
1601-1700	0	0	16	16
1701-1800	10	22	4	36
1801-1900	9	3	1	13
1901-2000	5	0	0	5
2001-2100	2	0	3	5
2101-2200	1	0	5	6
2201-2300	0	0	11	11
2301-2400	14	12	11	37
Total	111	95	149	355

ington usually were taken at approximately 0630, 1200, 1800, and 2400; and hauls from *Undaunted* at 0500, 1200, 1730, and 2400. At least some hauls were taken during every hour of the day.

EFFECTIVENESS OF SAMPLING FISH LARVAE IN DAYLIGHT HAULS AS COMPARED WITH NIGHT HAULS

Catches of fish larvae for selected families in day hauls compared to night hauls or to hauls taken within ± 1 hr of sunrise or sunset are summarized in Table 3. For all categories of larvae combined, the catch was 212.0 larvae per daytime haul and 480.4 larvae per night haul, a difference in catch of 2.27×. Hauls taken within ± 1 hr of sunrise or sunset had an average catch of 347.0 larvae, intermediate between day and night catches.

Difference between day and night collections was somewhat less than for ETP I; on that survey the average count of larvae in night hauls was 2.76× as many as in day hauls (Ahlstrom 1971, Table 4). On both surveys gonostomatid larvae had the most marked differences in catches between night hauls and day hauls: 4.3× as many, on the average, in night collections compared with day on ETP I, 2.9× as many in night collections on ETP II. Night-day differences in catch per haul of myctophid larvae were less marked between the two surveys: 3.0× on ETP I as compared with 2.6× on ETP II. Night-day differences in average catches of bathylagid larvae were similar on the two multivessel surveys: 1.5× as many per haul on the average, in night collections compared with day collections. Sternoptychid larvae, which were sampled almost as well in day hauls as in night hauls on ETP I, showed a somewhat greater night-day difference on ETP II: 1.7× for ETP II as compared with 1.2× for ETP I.

Scombrid larvae were taken in lesser numbers per haul in both day and night hauls on ETP II compared with ETP I; in contrast to ETP I, however, (where a night-day difference of 3.7× was observed) no difference was obtained in night and day collections on ETP II.

TABLE 3.—Comparison of occurrences (positive hauls) and catches (original counts) of fish larvae in day hauls, night hauls, and hauls taken within 1 hr of sunrise or sunset, summarized for selected families.

Family or group	Day hauls			Night hauls				Hauls within ± 1 hr of sunrise or sunset			Total hauls		
	Number positive hauls	Total larvae	Average number per occupancy ($\bar{D}$)	Number positive hauls	Total larvae	Average number per occupancy ($\bar{N}$)	$\bar{N}/\bar{D}$	Number positive hauls	Total larvae	Average number per occupancy	Number positive hauls	Total larvae	Average number per occupancy
Bathylagidae	114	1,802	13.1	110	2,607	20.2	1.5	74	1,482	16.8	298	5,891	16.6
Gonostomatidae	131	4,896	35.5	125	13,264	102.8	2.9	86	6,095	69.3	342	24,255	68.3
Sternoptychidae	104	2,005	14.5	104	3,136	24.3	1.7	69	2,244	25.5	277	7,385	20.8
Chauliodontidae	18	68	0.5	23	86	0.7	1.4	15	53	0.6	56	207	0.6
Idiacanthidae	58	211	1.5	70	307	2.4	1.6	53	277	3.1	181	795	2.2
Other stomiatoidei	78	412	3.0	83	447	3.5	1.2	54	248	2.8	215	1,107	3.1
Myctophidae	136	13,847	100.3	128	33,167	257.1	2.6	88	16,995	193.1	352	64,009	180.3
Paralepididae	84	851	6.2	95	1,110	8.6	1.4	68	574	6.5	247	2,535	7.1
Scopelarchidae	47	83	0.6	53	139	1.1	1.8	34	76	0.9	134	298	0.8
Melamphaidae	112	463	3.4	105	581	4.5	1.3	67	321	3.6	284	1,365	3.8
Bregmacerotidae	59	847	6.1	59	1,138	8.8	1.4	42	1,077	12.2	160	3,062	8.6
Exocoetidae	27	104	0.8	18	22	0.2	0.2	14	20	0.2	59	146	0.4
Trachypteridae	13	14	0.1	22	27	0.2	2.0	11	18	0.2	46	59	0.2
Apogonidae	21	112	0.8	26	94	0.7	0.9	19	77	0.9	66	283	0.8
Bramidae	20	29	0.2	28	43	0.3	1.5	19	24	0.3	67	96	0.3
Chiasmodontidae	31	60	0.4	43	106	0.8	2.0	26	71	0.8	100	237	0.7
Coryphaenidae	43	60	0.4	40	75	0.6	1.5	26	50	0.6	109	185	0.5
Nomeidae	83	483	3.5	85	642	5.0	1.4	61	335	3.8	229	1,460	4.1
Scombridae	14	92	0.7	25	94	0.7	1.0	16	62	0.7	55	248	0.7
Other identified	114	1,278	9.3	120	3,649	28.3	3.0	79	959	10.9	313	5,886	16.6
Unidentified	69	260	1.9	65	426	3.3	1.7	48	176	2.0	182	862	2.4
Disintegrated larvae	118	1,272	9.2	98	814	6.3	0.7	72	728	8.3	288	2,814	9.8
Total fish larvae	138	29,249	212.0	129	61,974	480.4	2.27	88	31,962	363.1	355	123,185	347.0

WATER TEMPERATURES ON EASTROPAC II

Water temperatures were available at 1-m intervals from the surface to about 750-m depth for each station at which an STD was used for determination of salinity and temperature. I selected three depths for tabulation and study: surface, 10 m, and 50 m. STD readings were available for 347 of the 355 plankton stations taken on ETP II. A chart of surface temperature for ETP II will be included in the EASTROPAC Atlas.

To facilitate discussion of distributions of fish larvae, I have found it convenient to divide the EASTROPAC area into quadrants with the north-south division at the equator and the east-west division at long 100°W. I will use these divisions when discussing distribution of temperatures on ETP II, except for separating out a narrow band of water at the equator (lat 2°N to 2°S). Within a quadrant the temperatures are summarized by 5° latitude, except near the equator (Table 4).

In some parts of the ETP II pattern, the thermocline was considerably deeper than 50 m, so that the temperature at 50 m was similar to that at the surface. At a few stations in the northeast quadrant, where the thermocline was almost at the surface, the temperature at 10 m was 5° to 10°C lower than at the surface. At most stations in this quadrant the thermocline was considerably shallower than 50-m depth, as attested by marked differences in temperature between the surface and 50 m (Table 5). Mixed layer depths on ETP II were illustrated in Blackburn, Laurs, Owen, and Zeitzschel (1970)—Figure 7 on page 27. A brief summary of the temperature structure is given by quadrant.

NORTHEAST QUADRANT, EXCEPT WITHIN 2° LATITUDE OF EQUATOR

Surface temperatures in this quadrant were high, ranging between 25.4° and 29.8°C (average 27.2°C). Temperatures at 10 m were usually the same or within ±0.5°C of the surface, although 10 stations showed differences of more than 1°C and 7 of those were 4.6° to 10.1°C lower. These marked differences are indications of very shallow thermoclines; five contiguous stations along long 88°W offshore from Puntarenas, Costa Rica, had such near-surface thermoclines.

At most stations the thermocline was shallower than 50 m; at 79 of 91 stations, the temperature at 50 m was 5° to 15°C lower than at the surface, and at half of these the temperature was between 10° to 15°C lower at 50 m.

NORTHWEST QUADRANT, EXCEPT WITHIN 2° LATITUDE OF EQUATOR

Surface temperatures in this quadrant, 24.8° to 29.7°C (average 27.6°C), were similar to those of the inshore quadrant. Highest surface temperatures, averaging 28.3°C, were encoun-

TABLE 4.—Range of temperatures at surface, 10 m, and 50 m summarized by 5° latitude or smaller intervals for both offshore (long 100°-119°W) and inshore (coast to long 98°W) for EASTROPAC II.

Latitude	Offshore: long 100°-119°W				Inshore: coast to long 98°W			
	No. stn.	Range in temperature (°C) at:			No. stn.	Range in temperature (°C) at:		
		Surface	10 m	50 m		Surface	10 m	50 m
15°-20°N	32	25.7-29.7	25.5-29.6	17.7-28.6	1	29.8	29.6	23.1
10°-15°N	30	26.3-29.8	26.0-29.4	16.7-27.9	23	26.4-29.7	19.7-29.6	14.0-26.7
5°-10°N	20	25.8-27.7	25.8-27.8	16.5-27.4	42	25.8-28.9	16.3-28.9	13.5-23.6
2°- 5°N	15	24.8-26.6	24.8-26.4	20.3-26.2	25	25.2-26.8	25.3-27.0	15.2-25.9
Total 2°-20°N	97	24.8-29.7	24.8-29.6	16.5-28.6	91	25.2-29.8	16.3-29.6	13.5-26.7
Equator 2°N-2°S	20	19.5-25.0	19.0-25.0	15.7-22.4	30	16.4-25.9	15.6-25.9	13.7-17.4
2°- 5°S	14	20.6-23.0	20.5-23.0	14.0-22.6	19	18.4-22.2	17.4-21.9	14.2-20.2
5°-10°S	16	22.9-24.9	22.7-24.9	22.4-24.9	30	16.3-21.5	16.3-21.5	14.6-21.4
10°-15°S	0	--	--	—	30	15.4-21.4	15.1-21.4	13.9-21.2
Total 2°-15°S	30	20.6-24.9	20.5-24.9	14.0-24.9	79	15.4-22.2	15.1-21.9	13.9-21.4

TABLE 5.—Summary of temperature differences within upper 50 m depth (differences in temperature at the surface and at two selected depths—10 m and 50 m) summarized by quadrants.

Area	No. stn.	Difference in temperature at the surface and at 10-m depth					Difference in temperature at the surface and at 50-m depth				
		0°C	0.1°-0.5°C	0.6°-1.0°C	1.1°-5.0°C	5.1°-10.1°C	0°C	0.1°-1.0°C	1.1°-5.0°C	5.1°-10.0°C	10.1°-15.0°C
NE Quadrant (lat 2°-16°N, coast to long 98°W)	90	38	39	3	4	6	0	2	9	40	39
NW Quadrant (lat 2°-20°N, long 100-119°W)	97	65	26	5	1	0	6	14	46	27	4
Equator (lat 2°N-2°S, coast to long 98°W)	30	19	8	1	2	0	0	0	10	19	1
Equator (lat 2°N-2°S, long 100-119°W)	20	9	9	2	0	0	0	1	13	6	0
SE Quadrant (lat 2°-15°S, coast to long 98°W)	79	61	15	2	1	0	20	31	27	1	0
SW Quadrant (lat 2°-10°S, long 100-119°W)	30	17	12	1	0	0	9	15	5	1	0

tered between lat 15° and 20°N. Temperatures at 10 m were usually the same as at the surface, and in only one instance was the difference as great as 1.3°C. Temperatures at 50 m were identical to, or within 1°C of, the surface temperatures at about 20% of the stations, all located between lat 2° and 10°N—these were stations with deep thermoclines. Temperature differences between the surface and 50 m exceeded 5°C at about 35% of the stations.

EQUATOR, LAT 2°N TO 2°S

Surface temperatures were variable, with 9.5°C range (16.4° to 25.9°C). Lowest surface temperatures, undoubtedly resulting from upwelling, were encountered seaward of the Galapagos Islands, between long 92° and 98°W, lat 0.5°N to 2.0°S, but cold water was also encountered farther offshore. Thermoclines were shallow at most stations inshore from the Galapagos Islands, the difference between surface and 50 m exceeded 5°C at about 63% of the stations, but the surface water was warmer than offshore.

SOUTHEAST QUADRANT, EXCEPT WITHIN 2° LATITUDE OF EQUATOR

Water temperatures were much lower in this quadrant than in the northeast quadrant. Few surface temperatures were as high as 20°C, and the average surface temperature was 18.7°C. The thermocline was usually deep. At 65% of the stations the temperature at 50 m was the same as that at the surface or was not more than 1°C colder.

SOUTHWEST QUADRANT, EXCEPT WITHIN 2° LATITUDE OF EQUATOR

Surface temperatures ranged from 20.6° to 24.9°C (average 21.0°C). Temperatures at 10 m were usually the same as that at surface or within 0.5°C. Temperatures at 50 m were identical to the surface at 30% of stations and within 1°C of the surface temperature at 80% of stations, indicative of a region of deep thermocline.

In summary, water temperatures were much higher north of the equator, than south of the equator. Surface temperatures averaged 8.5°C higher in the northeast quadrant than in the southeast quadrant. Offshore the differences were almost as great; surface temperatures averaged 6.6°C higher in the northwest quadrant than in the southwest quadrant.

As noted in the paper dealing with ETP I collections, information is mostly lacking on depth distribution of fish larvae in the eastern tropical Pacific. Because of the marked variation in depth of thermocline encountered in different

parts of the EASTROPAC pattern, ranging from near-surface to deep, it is anticipated that depth distribution of larvae will be markedly affected by the temperature structure. A carefully planned study of depth distribution of larvae in the eastern tropical Pacific in relation to temperature and thermocline depth is badly needed. Lacking this, it is difficult to meaningfully relate larval distributions to temperature.

A REVIEW OF SIGNIFICANT PAPERS DEALING WITH ADULT FISHES OF THE EASTROPAC AREA

A working knowledge of the adult fishes of an oceanic region is a necessary prerequisite to meaningful study of the fish larvae of that region. Most larval series, initially, are established by working backwards from larger identified specimens (late-larvae or early juveniles) to early-stage larvae. Until recently shore fishes of the eastern tropical Pacific were much better known than deep-sea fishes, e.g., studies by Meek and Hildebrand (1923, 1925, 1928) for Panama and Hildebrand (1946) for Peru. Shore fishes, however, were not an important element of the EASTROPAC ichthyoplankton.

A major contribution to our knowledge of eastern Pacific fishes was made by Garman (1899), who worked up the fishes collected on the *Albatross* Expedition of 1891 to the west coasts of Mexico, Central and South America, and off the Galapagos Islands. Garman dealt with 180 species of fish, most new to science; about a third of these were pelagic, oceanic fishes. Included among the latter are the two most common pelagic fishes, *Diogenichthys laternatus* and *Vinciguerria lucetia*, in the eastern tropical Pacific, based on their abundance as larvae.

The second oceanographic expedition of the *Pawnee* to the eastern Pacific in 1926 added materially to our knowledge of the deep-sea fishes. Several of the species described by Parr (1931) from these collections are common as larvae in EASTROPAC plankton hauls, including *Bathylagus nigrigenys, Diaphus pacificus, Lampanyctus idostigma, L. parvicauda,* and *Scopelarchoides nicholsi.*

The New York Zoological Society sponsored several expeditions to the eastern Pacific which stimulated papers on Pacific Myctophidae by Beebe and Vander Pyle (1944) and on ceratioid fishes by Beebe and Crane (1947). The paper on myctophids contains information on taxonomy, biology, and zoogeography of 24 species of myctophids of which none were new. The paper by Beebe and Crane on deep-sea ceratioid fishes dealt with 24 species belonging to six families, of which 10 were new.

The ceratioid fishes of the Gulf of Panama had received attention previously: the Danish research vessel *Dana* had occupied several very productive stations in the Gulf of Panama in 1922, from which Regan (1926) described 18 species of ceratioids, mostly new. Bertelsen (1951) reported taking early life history stages of 23 kinds of ceratioids from the Gulf of Panama in *Dana* collections from its round-the-world expedition of 1928-30.

Information on fishes off Peru was obtained on the Yale South American Expedition of 1953. Morrow (1957a) gave an annotated list of 104 shore fishes, 21 new to the Peruvian fauna, and Morrow (1957b) gave an annotated list of 18 mid-depth fishes.

Bussing (1965) reports on 15 pelagic trawl hauls made on *Eltanin* cruises taken off the South American coast in 1962 and 1963 between lat 3° and 35°S. The collections contained 100 species, representing 33 families. Four trawl hauls were made within the EASTROPAC area; only one yielded substantial numbers of specimens. This was *Eltanin* Station 34 at lat 7°45′ to 7°48′S, long 81°23′W, from which 45 species were obtained.

Haedrich and Nielsen (1966) provided annotated identifications of 32 species (21 families) of fishes from stomachs of *Alepisaurus* collected at 19 stations by exploratory longline fishing from the Japanese RV *Shoyo Maru.* Four collections were obtained within the EASTROPAC area, and the other 15 between lat 20° and 40°S.

Craddock and Mead (1970) reported on collections made along two transects through the

southern portion of the Peru Current off Chile at lat 34°S. They provide annotated identifications of 133 species. Although these transects were south of the EASTROPAC area, many of the species also occur in the EASTROPAC area.

Parin (1971) reports on collections of midwater fishes of the Peru Current zone collected on the fourth cruise of RV *Akademik Kurchatov*. He lists about 150 species representing 33 families. Collections were obtained between lat 5°N and 30°S, in a broad coastal band, extending offshore to long 90°W. Distributions are illustrated for 24 species.

In addition to the above, a number of references dealing with particular species of genera or families of eastern Pacific fishes are cited in the body of the text, or were referred to in Ahlstrom (1971).

NUMBER OF FISH LARVAE OBTAINED ON EASTROPAC II

Fish larvae were obtained in all collections (355) made with the 1-m plankton net on ETP II; counts of larvae per haul ranged from 1 to 2,864, and averaged 347. Four collections contained 10 or fewer larvae, and 22 collections contained 1,000 or more specimens in each (Table 6).

Abundance of fish larvae according to latitude and proximity to shore within the EASTROPAC pattern is summarized in Table 7. The same grouping of stations by latitude (5° except near the equator) and longitude (inshore-offshore) is used as in Table 4 (temperature summary table). Subtotals provide a rough separation into quadrants.

Larvae were taken in greatest abundance in the northeast quadrant, particularly between lat 5° and 10°N; in this latter area, with an average surface temperature of 27.1°C, larvae averaged 639 per haul. Larvae were less abundant in the southeast quadrant, with numbers decreasing southward and averaging only 118 larvae per haul between lat 10° and 15°S (average surface temperature, 18.1°C).

Larvae were much less abundant offshore, in the northwest quadrant, averaging slightly over 40% as many per haul as in the inshore (northeast) quadrant. Surface temperatures, however, were quite similar.

Near the equator (lat 2°N to 2°S), larvae were moderately abundant inshore (434 per haul), and the decrease in the abundance offshore was not as marked as in other areas (362 per haul). This is not surprising, since this was an area of upwelling.

In the southwest quadrant (lat 2° to 10°S, long 110° to 119°W), there was a decrease in abundance toward the south. However, this quadrant was poorly sampled on ETP II. When compared to inshore coverage of the same latitude (lat 2° to 10°S), abundance of larvae per haul averaged about 62% as many.

Fish larvae averaged more per haul on ETP II as compared with comparable coverage on ETP I, 347.0 versus 231.9 larvae per haul; the increase in abundance was reflected in all parts of the EASTROPAC pattern.

The majority of large collections of fish larvae were made at stations with shallow thermoclines and relatively high mixed layer water

TABLE 6.—Relative numbers of fish larvae obtained over the three vessel patterns occupied on EASTROPAC II; last column gives comparable counts for EASTROPAC I.

No. of fish larvae per haul	*Washington* 45.000 Series	*Undaunted* 46.000 Series	*Rockaway* 47.000 Series	All patterns — EASTROPAC II	Comparable Coverage — EASTROPAC I
0	0	0	0	0	4
1-10	1	0	3	4	6
11-100	29	16	27	72	122
101-1,000	78	72	107	257	214
1,001 and over	3	7	12	22	9
Total	111	95	149	355	355
Average no. larvae per haul	224.0	400.3	404.7	347.0	231.9

TABLE 7.—Total catches of fish larvae (actual counts) taken on EASTROPAC II summarized by latitude (5° except near equator) and longitude (offshore or inshore).

Latitude	Offshore: long 100°-119°W			Inshore: coast to long 98°W		
	Number stations occupied	Number of larvae per haul		Number stations occupied	Number of larvae per haul	
		Range	Mean		Range	Mean
15°-20°N	32	31-1,048	219.0	1	130	130.0
10°-15°N	30	58- 481	159.1	23	37-2,242	435.4
5°-10°N	21	21-1,128	237.4	42	61-2,864	639.1
2° -5°N	16	93-1,217	359.6	28	141-1,975	555.1
Total 2°-20°N	99	21-1,128	227.5	94	37-2,864	558.8
Equator 2°N-2°S	21	30-1,506	361.5	30	1-1,513	434.4
2°- 5°S	14	79- 817	268.5	20	6-1,061	431.4
5°-10°S	16	8- 472	178.2	30	27-1,002	287.3
10°-15°S	--	--	--	31	4- 579	118.0
Total 2°-15°S	30	8- 817	220.4	81	4-1,061	258.1
Grand total	150	8-1,506	244.8	205	1-2,864	421.8

temperatures. Over 60% of the larger collections of fish larvae (750 or more larvae) were taken at stations with mixed layer temperatures in excess of 26°C and mixed layer depths of 35 m or less.

Unfortunately, information is lacking on the depth distribution of fish larvae in the eastern tropical Pacific in relation to thermocline depth, hence it is not known whether most kinds were limited in depth distribution to the upper mixed layer, as reported for California Current waters (Ahlstrom, 1959).

KINDS OF FISH LARVAE OBTAINED ON EASTROPAC II

With some interesting exceptions, the same kinds of larvae were obtained on ETP II as on ETP I, and Table 8, the principal summary table covering ETP II larvae, contains essentially the same families as its counterpart for ETP I. The table lists 53 families and 6 composite categories including 3 orders or suborders and a catchall category—other identified. For the latter, composition by families is given in subsequent tables or in text discussions. Altogether, fish larvae of 82 families were represented in ETP II collections. As on ETP I, larvae of 10 families contributed over 90% (91.0 on ETP II) of the total; 9 of these families were among the first 10 on both EASTROPAC surveys and had similar rankings. The first 10 families on ETP II were as follows: Myctophidae, 52.0%; Gonostomatidae, 19.7%; Sternoptychidae, 6.0%; Bathylagidae, 4.8%; Bregmacerotidae, 2.5%; Paralepididae, 2.0%; Nomeidae, 1.2%; Melamphaidae, 1.1%; Engraulidae, 1.1%; and Idiacanthidae, 0.6%. Engraulidae is the only family on this list that did not rank among the first 10 on ETP I. The sole displacement from the previous list is the family Scombridae, which slipped in ranking from fifth in ETP I to twentieth in ETP II. Of the remaining 9%, 2.3% were too damaged (disintegrated) to identify, 0.7% could not be identified (these were mostly very small larvae), and the remainder, about 6%, belonged to the other 72 families.

The displacement of Scombridae from among the 10 most abundant families on ETP II left only one perciform family, Nomeidae, among those contributing 1% or more of the total. Only a moderate number of perciform families have become widely distributed in offshore oceanic waters. Among these, larvae of Gempylidae contributed 0.3% of the total on ETP II; Apogonidae, 0.2%; Chiasmodontidae, 0.2%; Coryphaenidae, 0.1%; Trichiuridae, 0.1%; and Bramidae, 0.1%.

The basic data on the kinds and number of fish larvae obtained in the 355 ETP II collections are contained in Appendix Tables 1 to 6. These are keyed to Table 8 and to other tables in this report.

The data presented in this paper represent but the first step in utilizing eggs and larvae collections for resource evaluation.

TABLE 8.—Occurrences and counts of fish larvae taken in oblique 1.0-m plankton hauls on the second multivessel EASTROPAC survey (EASTROPAC II), summarized by family or larger grouping and by research vessel.

Family or larger grouping[1]	Basic station data contained in Appendix Table no.		Distribution shown in Figure no.	*Washington* 45.000 Series		*Undaunted* 46.000 Series		*Rockaway* 47.000 Series		Total EASTROPAC II	
	By family or larger grouping	By genus or species		No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
1 Albulidae		4		0	0	0	0	2	9	2	9
*2 Clupeidae		4	3	0	0	7	185	2	85	9	270
*3 Engraulidae		4	3	4	15	2	3	29	1,342	35	1,360
*4 Argentinidae		3		14	21	14	32	4	5	32	58
*5 Bathylagidae	1	3	4	74	352	90	1,277	134	4,262	298	5,891
*6 Gonostomatidae	1	3	5-7	108	9,079	94	7,095	140	8,081	342	24,255
*7 Sternoptychidae	1			75	1,882	74	1,941	128	3,562	277	7,385
*8 Astronesthidae	3		5	10	16	15	30	17	28	42	74
*9 Chauliodontidae	1		8	10	25	10	15	36	167	56	207
*10 Idiacanthidae	1		9	49	275	62	219	70	301	181	795
*11 Other Stomiatoidei	1	3		60	245	64	219	86	570	210	1,034
12 Chlorophthalmidae				0	0	3	5	1	3	4	8
*13 Evermannellidae	3		10	9	47	7	19	1	1	17	67
*14 Myctophidae	1	2	3, 8, 11-14	111	9,546	95	21,082	146	33,381	352	64,009
15 Neoscopelidae				5	5	2	3	5	7	12	15
*16 Paralepididae	1	3		91	497	80	1,002	76	1,036	247	2,535
*17 Scopelarchidae	1			39	103	45	92	50	103	134	298
*18 Scopelosauridae	3		10	0	0	11	46	29	344	40	390
*19 Synodontidae	4		5	1	1	2	6	11	53	14	60
20 Alepisauridae				1	1	1	2	2	2	4	5
*21 Anguilliformes	5		14, 15	16	33	30	42	35	76	81	151
*22 Melamphaidae	1		16	79	262	83	408	122	695	284	1,365
*23 Trachichthyidae	3			0	0	0	0	11	70	11	70
24 Holocentridae				3	10	0	0	0	0	3	10
*25 Bregmacerotidae	1			63	379	47	1,624	50	1,059	160	3,062
26 Macrouridae				1	1	3	3	5	5	9	9
*27 Scomberesocidae	3		14	0	0	0	0	27	153	27	153
28 Exocoetidae	1			15	26	22	33	22	87	59	146
29 Trachypteridae	1			10	10	16	20	20	29	46	59
*30 Apogonidae	1			28	178	24	73	14	32	66	283
31 Balistidae	3			1	1	3	6	1	1	5	8
32 Blenniidae				0	0	0	0	5	6	5	6
33 Bramidae	1			21	31	17	24	29	41	67	96
*34 Carangidae	4		17	8	28	8	59	20	137	36	224
35 Carapidae	4			0	0	0	0	7	7	7	7
36 Chiasmodontidae	1			25	46	25	45	50	146	100	237
*37 Coryphaenidae	1			37	56	34	62	38	67	109	185
*38 Gempylidae		3	4	36	59	30	64	46	247	112	370
*39 Gobiidae	4			5	65	11	33	37	286	53	384
40 Labridae	4		10	9	21	9	10	14	26	32	57
41 Mugilidae	4			0	0	0	0	5	16	5	16
*42 Nomeidae	1			68	357	64	391	97	712	229	1,460
*43 Ophidiidae				0	0	7	9	31	72	38	81
44 Polynemidae	4			2	21	2	5	3	5	7	31
45 Pomacentridae	4			1	6	0	0	4	5	5	11
46 Sciaenidae	4			0	0	2	93	8	34	10	127
*47 Scombridae	1			15	70	24	89	16	89	55	248
48 Scorpaenidae	4			5	18	16	93	37	133	58	244
49 Serranidae	4			3	13	6	13	17	54	26	80
50 Sphyraenidae				0	0	1	2	1	8	2	10
*51 Tetragonuridae[2]		3	17	5	5	5	6	1	1	11	12
*52 Trichiuridae		3	4, 17	3	3	2	2	44	181	49	186
*53 Bothidae		4	8	7	19	28	307	35	364	70	690
*54 Cynoglossidae		4		2	5	16	109	38	248	56	362
55 Ostraciontidae	3			14	49	1	1	0	0	15	50
*56 Lophiiformes	6		18	25	42	33	56	56	145	114	243
*57 Other identified				7	11	3	3	13	37	23	51
58 Unidentified larvae	1			48	171	56	265	78	426	182	862
59 Disintegrated larvae	1			96	753	77	809	115	1,252	288	2,814
Total				111	24,859	95	38,032	149	60,294	355	123,185

[1] Categories preceded by an asterisk are discussed in the text.
[2] Discussed in text under 42, Nomeidae.

TABLE 9.—Standardized counts of fish larvae compared with unstandardized (original) counts, summarized for selected families (see Appendix Table 8 for standardized haul factors).

Family or larger grouping	Standardized counts					Unstandardized counts	
	45.000 series	46.000 series	47.000 series	Total standardized counts	Percentage of total	Total unstandardized counts	Percentage of total
Bathylagidae	1,132	3,569	14,427	19,128	4.8	5,891	4.8
Gonostomatidae	31,525	19,347	26,717	77,589	19.5	24,255	19.7
Sternoptychidae	6,529	5,977	12,321	24,827	6.3	7,385	6.0
Chauliodontidae	97	43	589	729	0.2	207	0.2
Idiacanthidae	901	699	996	2,596	0.7	795	0.6
Other Stomiatoidei	914	732	2,061	3,707	0.9	1,107	0.9
Myctophidae	31,015	62,775	111,787	205,577	51.8	64,009	52.0
Paralepididae	1,712	2,724	3,511	7,947	2.0	2,535	2.1
Scopelarchidae	350	281	342	973	0.2	298	0.2
Melamphaidae	818	1,227	2,223	4,268	1.1	1,365	1.1
Bregmacerotidae	1,259	5,772	3,210	10,241	2.6	3,062	2.5
Exocoetidae	78	104	245	427	0.1	146	0.1
Trachypteridae	32	63	93	188	<0.1	59	<0.1
Apogonidae	636	228	110	974	0.2	283	0.2
Bramidae	99	77	138	314	0.1	96	0.1
Chiasmodontidae	161	123	501	785	0.2	237	0.2
Coryphaenidae	185	194	227	606	0.2	185	0.2
Nomeidae	1,132	1,235	2,345	4,712	1.2	1,460	1.2
Scombridae	237	296	284	817	0.2	248	0.2
Other identified	1,704	3,893	13,204	18,801	4.7	5,886	4.8
Unidentified	590	827	1,274	2,691	0.7	862	0.7
Disintegrated larvae	2,604	2,405	4,255	9,264	2.3	2,814	2.3
Total fish larvae	83,710	112,591	200,860	397,161	100.0	123,185	100.1

Relative abundance of fish as larvae is not necessarily proportional to their relative abundance as adults. A number of parameters would have to be evaluated if counts of eggs and larvae of a species are to be used in determining the biomass of adult populations. These include fecundity (preferably given as number of eggs spawned in relation to fish weight—such as number of eggs spawned per gram of female weight); egg size, which influences size and state of development at hatching; duration of time spent in plankton both as egg stage and as larva as related to temperature of development; mortality rates during embryonic and larval stages; size at transformation; length of spawning season; age structure of population; etc.

I am assuming that the relative abundances of larvae of a given species are comparable from cruise to cruise in the EASTROPAC area. I am further assuming that comparisons of relative abundance within a family, as for example among myctophid or among scombrid larvae, will reflect their relative abundance as adults within reasonable limits. I, however, would caution against taking comparisons between families too literally until essential parameters are evaluated for each.

Actual counts of larvae rather than standardized values are used in tabulations throughout the paper, except Table 9. Table 9 compares summations of larvae of selected families based on standardized values with summations based on actual counts. These families make similar percentage contributions to the larval catch whether based on standardized counts or actual counts.

COMPARISON OF COMPOSITION AND RELATIVE ABUNDANCE OF LARVAE IN EASTROPAC II AND EASTROPAC I COLLECTIONS

In order to keep comparisons between the two EASTROPAC multivessel cruises completely relevant, the following stations lacking counterparts in ETP II were omitted from ETP I summations: Stations 11.146 to 11.328 of the outer pattern occupied by *Argo,* Stations 12.122 to 12.164 of the adjacent pattern occupied by *David Starr Jordan,* and Stations 13.095 to 13.155 of the next to inner pattern occupied by *Rockaway.* The remaining stations, by happy coincidence, total 355, are identical to the

TABLE 10.—Comparison of occurrences and relative abundance of fish larvae on EASTROPAC II (355 stations) with comparable coverage on EASTROPAC I (355 stations) summarized by family or larger grouping.

Family or larger grouping	EASTROPAC II			EASTROPAC I		
	No. positive hauls	No. larvae	Average no. per haul	No. positive hauls	No. larvae	Average no. per haul
Clupeidae	9	270	0.8	10	81	0.2
Engraulidae	35	1,360	3.8	10	205	0.6
Argentinidae	32	58	0.2	38	81	0.2
Bathylagidae	298	5,891	16.6	275	4,742	13.4
Gonostomatidae	342	24,255	68.3	333	18,380	51.8
Sternoptychidae	277	7,385	20.8	240	4,923	13.9
Astronesthidae	42	74	0.2	11	12	<0.1
Chauliodontidae	56	207	0.6	59	124	0.3
Idiacanthidae	181	795	2.2	132	855	2.4
Other Stomiatoidei	210	1,034	2.9	157	428	1.2
Chloropthalmidae	4	8	<0.1	1	4	<0.1
Evermannellidae	17	67	0.2	10	13	<0.1
Myctophidae	352	64,009	180.3	346	39,249	110.6
Paralepididae	247	2,535	7.1	218	1,456	4.1
Scopelarchidae	134	298	0.8	109	273	0.8
Scopelasauridae	40	390	1.1	6	13	<0.1
Synodontidae	14	60	0.2	10	41	0.1
Anguilliformes	81	151	0.4	66	138	0.4
Melamphaidae	284	1,365	3.8	235	703	2.0
Trachypteridae	11	70	0.2	0	0	0
Bregmacerotidae	160	3,062	8.6	132	1,587	4.5
Scomberesocidae	27	153	0.4	1	1	<0.1
Exocoetidae	59	146	0.4	66	164	0.5
Trachypteridae	46	59	0.2	33	35	0.1
Apogonidae	66	283	0.8	37	135	0.4
Balistidae	5	8	<0.1	2	3	<0.1
Bramidae	67	96	0.3	40	49	0.1
Carangidae	36	224	0.6	31	183	0.5
Carapidae	7	7	<0.1	3	3	<0.1
Chiasmodontidae	100	237	0.7	48	97	0.3
Coryphaenidae	109	185	0.5	67	97	0.3
Gempylidae	112	370	1.0	59	110	0.3
Gobiidae	53	384	1.1	60	530	1.5
Labridae	32	57	0.2	28	40	0.1
Mugilidae	5	16	<0.1	5	9	<0.1
Nomeidae	229	1,460	4.1	159	900	2.5
Polynemidae	7	31	0.1	5	11	<0.1
Sciaenidae	10	127	0.4	4	12	<0.1
Scombridae	55	248	0.7	163	1,840	5.2
Scorpaenidae	58	244	0.7	47	162	0.5
Serranidae	26	80	0.2	26	252	0.7
Sphyraenidae	2	10	<0.1	3	3	<0.1
Tetragonuridae	11	12	<0.1	2	3	<0.1
Trichiuridae	49	186	0.5	19	48	0.1
Bothidae	70	690	1.9	56	199	0.6
Cynoglossidae	56	362	1.0	63	304	0.9
Lophiiformes	114	243	0.7	108	214	0.6
Other identified	76	247	0.7	--	159	0.4
Unidentified larvae	182	862	2.4	170	723	2.0
Disintegrated larvae	288	2,814	7.9	291	2,725	7.7
Total larvae	355	123,185	347.0	351[1]	82,319	231.9

[1] Total stations 355 of which 351 contained larvae (positive hauls), 4 were negative.

count of stations occupied on ETP II. Hence, comparisons between the two cruises can be based on either the average number of larvae per haul or on "total numbers of larvae" of each category inasmuch as equal numbers of stations contributed to the totals.

Comparisons of occurrence and relative abundance of fish larvae in the ETP II pattern (all stations) with comparable coverage for ETP II are summarized by family or larger groupings in Table 10.

Nearly 50% more fish larvae were obtained per haul, on the average, in ETP II (347.0 larvae) as compared with ETP I (231.9 larvae). The larvae of most families of fishes were taken in larger numbers on ETP II than on ETP I, and larvae of several families were taken in markedly larger numbers. The striking exception to this trend was afforded by scombrid larvae; only 13.5% as many scombrid larvae were obtained in ETP II collections as in similar coverage of ETP I.

Families showing the largest increase in total numbers of larvae on ETP II compared with ETP I included Engraulidae (1,360 to 205 larvae), Scomberesocidae (153 to 1 specimen), Scopelosauridae (390 to 13 larvae), Evermannellidae (67 to 13 larvae), Astronesthidae (75 to 13 larvae), Trachichthyidae (70 to 0 larvae), Sciaenidae (127 to 12 larvae), Trichiuridae (186 to 48 larvae), Gempylidae (370 to 110 larvae), and Clupeidae (270 to 81 larvae). For the majority of these, the increase in relative abundance of larvae was most marked in the inner pattern occupied by *Rockaway*. The species compositions involved in these increases, when known, are discussed later under the respective families.

For the majority of families, however, the increase in abundance of larvae on ETP II was moderate, seldom as much as double; for a third of the families, counts of larvae were not much different during the two contrasting periods of the year; thus the similarity in abundance of larvae during the two periods is the striking feature of this comparison.

COMPARISON WITH EASTROPAC MONITORING CRUISES

The portion of the eastern tropical Pacific pattern that could be covered by a single research vessel on surveys averaging 45 days was occupied at bimonthly intervals on four monitoring cruises by *David Starr Jordan*. The cruises were numbered as follows: 20.000 series for the April-May 1967 monitoring cruise, 30.000 series for the June-July monitoring cruise, 50.000 for the October-November 1967 monitoring cruise, and 60.000 for the December 1967-January 1968 monitoring cruise. The monitoring pattern is shown superimposed on ETP II stations in Figure 2; it consisted of four station lines all ending at lat 3°S. The outer line along long 119°W extended from lat 20°N, the inner line along long 98°W, off the Mexican coast (ca. lat 17°N). The two middle lines along long 105° and 112°W were doglegs veering coastward from about lat 12° or 13°N—one line ending up off Manzanillo, Mexico, and the other off Acapulco, Mexico.

Coverage equivalent to the monitoring pattern was determined for ETP I and II. For ETP I the following stations were occupied: 11.022 to 11.118 (35), 12.002 to 12.109 (50), 12.209 to 12.264 (24), and 13.187 to 13.265 (28); total 137 stations. For ETP II comparable coverage was obtained from Stations 45.016 to 45.114 (41), 45.191 to 45.365 (37), 46.002 to 46.069 (36), and 46.079 to 46.132 (27); total 141 stations.

COMPARISON OF LARVAL COMPOSITION IN MONITORING PATTERN VERSUS LARGER EASTROPAC PATTERN

In Table 11 a comparison is made for both ETP I and ETP II of the average number of larvae per haul and percentage contribution of larvae of the more important fish families in the monitoring pattern as compared with the total pattern occupied on ETP II.

The correspondence between relative abundance and composition of larvae in the monitoring pattern as compared with the larger ETP pattern is closer for ETP I collections than ETP II. The average abundance of larvae in the monitoring pattern on ETP I was 92% as large as for the larger ETP I pattern (equivalent to the coverage obtained on ETP II). The more abundant kinds of larvae—myctophids, gonostomatids, and sternoptychids—had similar average abundances per haul and similar percentage contributions in the monitoring pattern as compared with the more extensive ETP I coverage. Of the remaining seven families used in this com-

TABLE 11.—Comparison of relative abundance of fish larvae (average number per haul) in the monitoring pattern as compared with the total pattern occupied on EASTROPAC II and equivalent EASTROPAC I for more abundant families.

	EASTROPAC II						EASTROPAC I					
	Monitoring pattern (141 hauls)			Total pattern (355 hauls)			Monitoring pattern (137 hauls)			Pattern equivalent to total EASTROPAC II (355 hauls)		
Family	Average no. per haul	%	Rank	Average no. per haul	%	Rank	Average no. per haul	%	Rank	Average no. per haul	%	Rank
Myctophidae	116.4	45.6	1	180.3	52.0	1	104.9	49.0	1	110.6	47.7	1
Gonostomatidae	77.9	30.5	2	68.3	19.7	2	48.6	22.7	2	51.8	22.3	2
Sternoptychidae	12.8	5.0	3	20.8	6.0	3	14.2	6.6	3	13.9	6.0	3
Bathylagidae	4.9	1.9	5	16.6	4.8	4	6.4	3.0	5	13.4	5.8	4
Bregmacerotidae	3.4	1.3	7	8.6	2.5	5	6.6	3.1	4	4.5	1.9	6
Paralepididae	8.2	3.2	4	7.1	2.0	6	4.8	2.3	6	4.1	1.8	7
Nomeidae	4.2	1.7	6	4.1	1.2	7	3.6	1.7	7	2.5	1.1	8
Melamphaidae	2.9	1.1	9	3.8	1.1	8	1.5	0.7	10	2.0	0.9	10
Idiacanthidae	3.0	1.2	8	2.2	0.6	10	2.8	1.3	8	2.4	1.0	9
Scombridae	0.6	0.2	10	0.7	0.2	ca. 20	2.4	1.1	9	5.2	2.2	5
Other	20.8	8.2		34.5	9.9		18.1	8.5		21.5	9.3	
Total	255.1	99.9		347.0	100.0		213.9	100.0		231.9	100.0	

parison, four were taken in somewhat higher numbers in the monitoring pattern and three in the more extensive ETP I coverage. Among the latter, less than half as many scombrid larvae were taken per haul in the smaller pattern as compared with the larger.

The average abundance of larvae in the monitoring pattern on ETP II was only 73.5% as many as for the total ETP II pattern. Larvae of three families were slightly more abundant in the monitoring pattern than in the total ETP II pattern, including Gonostomatidae, Paralepididae, and Idiacanthidae; larvae of Scombridae and Nomeidae were about equally abundant in the two patterns. Four families of fishes, however, including Myctophidae and Sternoptichidae, were less abundant in the monitoring pattern as compared with the total ETP II pattern. Caution has to be exercised in the applications made of data from the monitoring pattern alone.

TEMPORAL CHANGES IN ABUNDANCE IN MONITORING PATTERN

Data from six successive bimonthly coverages of the monitoring patterns are exceptionally useful for determining the annual reproductive cycles of fishes in tropical waters. Data on relative abundance (average number per haul) are summarized for the 10 most common families in Table 12 and for selected genera and species in Table 13. The time period covered by each of the six surveys is indicated in these tables, and will be used for identifying cruises in the discussion.

The first thing to note is the range in abundance of total larvae on the six cruises: the highest abundance, 255.1 larvae per haul (August-September) was slightly less than double the lowest abundance, 133.1 larvae per haul in December-January. Range in abundance of larvae of each of the 10 families during the yearly cycle will be briefly discussed.

Myctophidae ranked first in all cruises, although barely so in the cruise made during June-July. The highest average number of larvae per haul, 116.4, obtained in August-September was almost double the lowest value, 58.7 larvae obtained in December-January. Myctophid larvae were as low as 37.9% of the total larvae (June-July), as high as 57.1% (October-November), and had an overall percentage contribution of 47.5%.

Gonostomatidae ranked second in all cruises; the lowest abundance per haul, 32.6 larvae in October-November, was less than half the highest value, 77.9 larvae per haul in August-September. Percentage contribution ranged between 18.5% (October-November) and 37.7% (June-July) and averaged 26.9%.

Sternoptychidae ranked third in abundance

TABLE 12.—Relative abundance and percentage contribution of fish larvae of the 10 most common families within that portion of EASTROPAC area covered on six successive bimonthly cruises between February 1967 and January 1968.

Family	ETP multivessel I[1] (Feb.-Mar.)		ETP monitoring cruise #20 (Apr.-May)		ETP monitoring cruise #30 (June-July)		ETP multivessel II[2] (Aug.-Sept.)		ETP monitoring cruise #50 (Oct.-Nov.)		ETP monitoring cruise #60 (Dec.-Jan.)		Six cruises - ETP monitoring area	
	Average no. per haul	%	Average no. per haul	%	Average no. per haul	%	Average no. per haul	%	Average no. per haul	%	Average no. per haul	%	Average no. per haul	%
Myctophidae	104.9	49.0	100.4	50.7	67.6	37.9	116.4	45.6	100.7	57.1	58.7	44.1	91.2	47.5
Gonostomatidae	48.6	22.7	50.6	25.6	67.3	37.7	77.9	30.5	32.6	18.5	33.7	25.3	51.6	26.9
Sternoptychidae	14.2	6.6	17.1	8.6	9.5	5.3	12.8	5.0	13.5	7.6	12.9	9.7	13.3	7.0
Bathylagidae	6.4	3.0	3.9	2.0	2.9	1.6	4.9	1.9	3.2	1.8	2.6	2.0	4.0	2.1
Paralepididae	4.8	2.3	4.1	2.1	5.3	3.0	8.2	3.2	3.2	1.8	4.8	3.6	5.1	2.7
Nomeidae	3.6	1.7	3.5	1.8	5.1	2.9	4.2	1.7	1.5	0.9	2.4	1.8	3.4	1.8
Bregmacerotidae	6.6	3.1	1.3	0.7	2.6	1.4	3.4	1.3	3.1	1.7	2.4	1.8	3.2	1.7
Idiacanthidae	2.8	1.3	2.9	1.5	2.0	1.1	3.0	1.2	1.1	0.6	1.5	1.1	2.2	1.1
Melamphaidae	1.5	0.7	1.8	0.9	1.6	0.9	2.9	1.1	1.7	1.0	1.3	1.0	1.8	0.9
Scombridae	2.4	1.1	1.4	0.7	1.0	0.6	0.6	0.2	1.3	0.8	1.4	1.1	1.4	0.7
Other	18.1	8.5	10.8	5.4	13.5	7.6	20.8	8.2	14.5	8.2	11.4	8.5	14.8	7.7
Total	213.9	100.0	197.8	100.0	178.4	100.0	255.1	99.9	176.4	100.0	133.1	100.0	192.0	100.1

[1] ETP I —stations 11.022-11.118 (35), 12.002-12.109 (50), 12.209-12.264 (24), and 13.187-13.265 (28).
[2] ETP II — stations 45.016-45.114 (41), 45.191-45.365 (37), 46.002-46.069 (36), and 46.079-46.132 (27).

in all cruises. The average abundance per haul ranged from 9.5 larvae (June-July) to 17.1 (April-May), a range of less than two times.

Bathylagid smelts were represented in the monitoring pattern by a single species, *Bathylagus nigrigenys* Parr. Average abundance of larvae per haul ranged from 2.6 (December-January) to 6.4 (February-March) and averaged 4.0 larvae. Larvae of Bathylagidae usually ranked fifth in abundance.

Paralepididae usually ranked fourth in relative abundance; the lowest average abundance per haul was 3.2 larvae in October-November, and the highest was 8.2 larvae in August-September.

Nomeidae ranked variously fifth to eighth in relative abundance, with an overall ranking of sixth. The range in average abundance per haul was from 1.5 (October-November) to 5.1 larvae (June-July) and averaged 3.4 larvae.

Bregmacerotidae showed the widest variation in abundance, 1.3 larvae (April-May) to 6.6 larvae (February-March); consequently they ranked variously between fourth and tenth in relative abundance. Larvae of the most common species of *Bregmaceros* within the monitoring pattern, *B. bathymaster*, tend to cluster with occasional samples having rather large numbers of larvae. Variability in sampling due to chance encounters of clusters of larvae could be of greater magnitude than that resulting from actual changes in reproductive activity during the year.

Idiacanthidae, usually ranked eighth in abundance per haul from 1.1 (October-November) to 2.9 larvae (April-May), with an overall average of 2.2 larvae per haul.

Melamphaidae ranked variously between seventh and tenth, with an overall rank of ninth. The lowest abundance, 1.3 larvae per haul in December-January, was less than half the highest, 2.9 larvae in August-September.

Scombridae in the monitoring area ranked either ninth or tenth in relative abundance of larvae on all cruises; the lowest average abundance, 0.6 larvae per haul in August-September, is only a fourth of the highest average value, 2.4 larvae in February-March.

Larvae of these 10 families made up over 92% of the fish larvae in the monitoring pattern. In all instances, larvae of all principal families were taken throughout the year. The spread between the highest and lowest abundance values for larvae of these principal families of fishes was usually less than three times, and for Myctophidae and Sternoptychidae, was less than double.

A similar seasonal pattern of abundance was observed for individual genera or species (Table 13). I found it helpful to arrange the 18 ge-

TABLE 13.—Relative abundance (average number per haul) of pelagic fish larvae of selected genera and species within that portion of EASTROPAC area covered on six successive bimonthly cruises between February 1967 and January 1968.

Genus or species	ETP multi-vessel I (Feb.-Mar.)	ETP monitor cruise #20 (Apr.-May)	ETP monitor cruise #30 (June-July)	ETP multi-vessel II (Aug.-Sept.)	ETP monitor cruise #50 (Oct.-Nov.)	ETP monitor cruise #60 (Dec.-Jan.)	Range	Average six cruises
	Average number per haul							
Bathylagus nigrigenys	6.4	3.9	2.9	4.9	3.2	2.6	2.6- 6.4	4.0
Cyclothone spp.	3.7	3.0	3.7	3.0	1.2	2.7	1.2- 3.7	2.9
Diplophos taenia	0.6	0.4	0.6	0.6	0.7	0.4	0.4- 0.7	0.6
Vinciguerria lucetia	43.3	45.8	62.5	71.9	30.3	30.0	30.0- 71.9	47.3
Chauliodus sp.	0.4	0.1	0.1	0.2	0.2	0.2	0.1- 0.4	0.2
Idiacanthus sp.	2.8	2.9	2.0	3.0	1.1	1.5	1.1- 3.0	2.2
Bathophilus filifer	0.9	0.6	0.6	1.3	0.6	0.9	0.6- 1.3	0.8
Diogenichthys laternatus	51.1	63.0	37.4	68.6	62.2	31.8	31.8- 68.6	52.4
Gonichthys tenuiculus	0.7	0.8	0.3	0.7	0.5	0.2	0.2- 0.8	0.5
Hygophum atratum	2.5	1.0	1.5	1.5	1.4	1.1	1.0- 2.5	1.5
Hygophum proximum	3.0	2.7	2.0	2.7	3.0	1.1	1.1- 3.0	2.4
Notolychnus valdiviae	2.8	2.4	2.0	2.0	1.6	1.5	1.5- 2.8	2.0
Notoscopelus resplendens	0.9	0.9	0.5	1.1	0.6	1.0	0.5- 1.1	0.8
Symbolophorus evermanni	1.4	0.4	1.0	1.9	1.2	1.0	0.4- 1.9	1.2
Triphoturus sp.	0.9	0.8	0.5	0.8	0.3	0.3	0.3- 0.9	0.6
Auxis spp.	2.2	1.1	0.7	0.5	1.1	1.1	0.5- 2.2	1.1
Coryphaena spp.	0.3	0.5	0.7	0.7	0.3	0.2	0.2- 0.7	0.4
Howella pammelas	0.8	1.1	1.3	1.6	0.6	0.4	0.4- 1.6	1.0
All others	89.2	66.4	58.1	88.1	66.3	55.1	55.1- 89.2	70.5
Total	213.9	197.8	178.4	255.1	176.4	133.1	133.1-255.1	192.4

nera and species of this table according to the magnitude of the seasonal change in abundance that each displayed.

Seasonal range in relative abundance between highest and lowest average number of larvae per haul:

Less than 2×: *Notolychnus valdiviae*

2.1 to 3×: *Bathylagus nigrigenys, Diplophos taenia, Vinciguerria lucetia, Idiacanthus* sp., *Bathophilus filifer, Diogenichthys laternatus, Hygophum atratum, Hygophum proximum, Notoscopelus resplendens, Triphoturus* sp.

3.1 to 4×: *Cyclothone* spp., *Chauliodus* sp., *Gonichthys tenuiculus, Coryphaena* spp., *Howella pammelas*

4.1 to 5×: *Symbolophorus evermanni, Auxis* spp.

Larvae of the above 18 genera and species were taken on all cruises throughout the year. Obviously, reproduction is a continuous process for all of these, varying in amount at different seasons of the year and at different latitudes, but never stopping entirely.

Larvae of two species dominated the collections from the monitoring pattern: those of the myctophid *Diogenichthys laternatus* and of the gonostomatid, *Vinciguerria lucetia*. Together these two species made up 44 to 56% of the total larvae in the monitoring pattern (Table 14).

The highest average abundance of larvae of the lanternfish, *Diogenichthys laternatus,* 68.6 larvae in August-September, was 2.5× as much as the lowest average abundance, 31.8 larvae in December-January. Larvae of this species ranked first in abundance between October and May, but were less abundant than larvae of *Vinciguerria lucetia* during June-September. Larvae of *Vinciguerria lucetia* had a range of 2.4× between their highest average abundance per haul, 71.9 larvae in August-September, and lowest, 30.0 larvae in December-January. A small but consistent change in abundance with season is evident for this species, with the peak period in June-September, the minimal period in October-January, and intermediate abundance of larvae in February-May.

The monitoring cruises were valuable in permitting us to establish the seasonal patterns of

TABLE 14.—Percentage contributions of larvae of the two most abundant species to the total catch of larvae in the monitoring pattern.

Cruise designation	Time of survey	Percentage contribution of larvae of		
		Vinciguerria lucetia	*Diogenichthys laternatus*	Combined
EASTROPAC I	Feb.-Mar.	20.2	23.9	44.1
20.000 series	Apr.-May	23.2	31.8	55.0
30.000 series	June-July	35.0	21.0	56.0
EASTROPAC II	Aug.-Sept.	28.6	26.9	55.1
50.000 series	Oct.-Nov.	17.2	35.3	52.5
60.000 series	Dec.-Jan.	22.5	23.9	46.4
	Annual	24.6	27.2	51.8

reproduction in oceanic, tropical fishes. Except for this, little more was gained from the repeated coverages that was not evident from any one of the six coverages. The same species composition was observed in all six cruises, and even the relative abundance of the various constituents did not change much. The similarity between cruises also extended to the geographic distributions of the various constituents which changed but little over time.

COMPARISON WITH RV *OCEANOGRAPHER* ZIG-TRANSECT

Although the average number of larvae per haul was almost identical for the *Oceanographer* collections and equivalent ETP II collections, 488.5 versus 487.8 larvae, and the kinds of larvae obtained were strikingly similar, the relative abundance of several categories was somewhat more variable than in the monitoring pattern (Table 15).

Similarities and differences in relative abundance of larvae during the two coverages can be shown from a consideration of the 10 families with highest abundance in the *Oceanographer* collections (Table 16).

Myctophidae.—The difference in relative abundance of Myctophidae larvae between *Oceanographer* and ETP II collections, 194.1 versus 273.9 larvae per haul, is almost entirely due to difference in relative abundance of larvae of *Diogenichthys laternatus*. Over 50% of *D. laternatus* larvae on ETP II were taken in four contiguous stations between lat 5°40′ and 7°44′N, with three collections exceeding 1,000 larvae and the largest with 2,505 larvae. Interestingly, the two *Oceanographer* collections containing more than 1,000 *D. laternatus* larvae were taken between lat 6° and 7°N; these were the only two stations occupied between lat 5°40′ and 7°44′N by *Oceanographer* in contrast to four collections from this rich area on ETP II.

Gonostomatidae.—The difference in relative abundance of Gonostomatidae larvae in the two occupancies of the zig-transect was again due principally to a single species, *Vinciguerria lucetia*. Although twice as many larvae of this species were taken in *Oceanographer* collections, an examination of the station record revealed that one collection, OP.036 with 2,046 larvae, accounted completely for the difference.

Clupeidae.—It is necessary to examine the species composition to evaluate differences between the two coverages (Table 17). Larvae of the sardine, *Sardinops sagax*, were taken in six contiguous stations near the Galapagos on ETP II, and averaged 29 larvae per positive haul, whereas only 1 sardine larva was obtained from the same area by *Oceanographer*. This species appears to have a period of peak spawning with reduced reproduction at other periods of the year. The contrast between the two collections of thread herring, *Opisthonema* sp., made at the station nearest the Mexican coast along long 92°W is the largest observed in EASTROPAC collections—2,730 larvae in the *Oceanographer* sample versus one larva in the ETP II collection. The larvae in the *Oceanographer* collection were intermediate-sized, 6 to 12.5 mm. Even allowing for the circumstance that clupeid larvae often occur in patches, this exceptionally large collection of larvae must have been obtained at a peak period of spawning of thread herring.

Bathylagidae.—Larvae of the two species of bathylagid smelts that occur in the area covered by the zig-transect, were similar in distribution and relative abundance in the two coverages. Larvae of *Bathylagus nigrigenys* were taken in all but three collections on each coverage, and average abundance per haul was almost identical, 26.3 versus 26.6 larvae (Table 17). Larvae of *Leuroglossus stilbius urotranus* had a more restricted distribution on both coverages, occurring between about 7°S and the equator, at sta-

TABLE 15.—Comparison of composition of catches of fish larvae in *Oceanographer* zig-transect, occupied in November-December 1967, with equivalent coverage by EASTROPAC II vessels during August-September 1967.

Family or larger grouping	*Oceanographer* (50 stations)			Equivalent ETP II coverage (48 stations)		
	No. positive hauls	No. larvae	Average no. per haul	No. positive hauls	No. larvae	Average no. per haul
Clupeidae	2	2,737	54.7	7	185	3.9
Engraulidae	6	760	15.2	15	381	7.9
Argentinidae	0	0	0	2	2	<0.1
Bathylagidae	47	2,308	46.2	45	2,005	41.8
Gonostomatidae	47	4,386	87.7	45	2,386	49.7
Sternoptychidae	39	976	19.5	40	1,093	22.8
Chauliodontidae	16	47	0.9	9	19	0.4
Idiacanthidae	15	27	0.5	28	58	1.2
Other stomiatoidei	28	209	4.2	32	274	5.7
Myctophidae	50	9,706	194.1	47	13,149	273.9
Paralepididae	28	556	11.1	25	320	6.7
Scopelarchidae	15	138	2.8	9	36	0.8
Scopelarsauridae	11	14	0.3	19	32	0.7
Synodontidae	1	3	0.1	3	7	0.1
Anguilliformes	10	18	0.4	16	23	0.5
Melamphaidae	43	243	4.9	40	274	5.7
Bregmacerotidae	1	470	9.4	9	1,455	30.3
Macrouridae	3	3	0.1	4	4	0.1
Exocoetidae	5	16	0.3	6	11	0.2
Scomberesocidae	1	1	<0.1	6	7	0.1
Trachypteridae	7	11	0.2	8	11	0.2
Apogonidae	1	1	<0.1	5	14	0.3
Bramidae	13	22	0.4	7	10	0.2
Carangidae	2	354	7.1	5	56	1.2
Chiasmodontidae	27	65	1.3	13	38	0.8
Coryphaenidae	8	8	0.2	8	13	0.3
Gempylidae	7	21	0.4	9	30	0.6
Gobiidae	6	42	0.8	12	35	0.7
Labridae	3	3	0.1	3	3	0.1
Nomeidae	37	185	3.7	27	155	3.2
Ophidiidae	6	10	0.2	5	6	0.1
Sciaenidae	4	34	0.7	4	96	2.0
Scombridae	7	82	1.6	10	41	0.9
Scorpaenidae	9	14	0.3	11	86	1.8
Serranidae	2	28	0.6	6	9	0.2
Sphyraenidae	1	1	<0.1	1	2	<0.1
Trichiuridae	4	4	0.1	8	10	0.2
Bothidae	14	67	1.3	17	227	4.7
Cynoglossidae	7	164	3.3	10	99	2.1
Lophiiformes	20	39	0.8	13	23	0.5
Other identified	6	104	2.1	12	23	0.5
Unknown larvae	21	53	1.1	21	100	2.1
Disintegrated larvae	42	488	9.8	42	606	12.6
Total larvae	50	24,417	488.5	48	23,414	487.8

tions occupied shoreward of the Galapagos Islands; the average abundance per haul was slightly higher in *Oceanographer* collections—19.9 versus 15.1 larvae.

Engraulidae—Larvae of *Engraulis ringens* were taken in more collections on ETP II (Table 17), but in lesser numbers per positive haul than in *Oceanographer* collections. The spawning period of the Peruvian anchovy is mostly between August and February (Einarsson and Rojas de Mendiola, 1967); both coverages were within this period of the year. Larvae of other engraulids were taken at the inner station off Mexico in both coverages, but in markedly larger numbers by *Oceanographer*. Larvae of Sternoptychidae, Melamphaidae, and Paralepididae had similar frequency of occurrence in the two coverages (Table 16); differences in relative abundance were small to moderate.

Carangid larvae were taken in more collec-

TABLE 16.—Comparison of occurrence and average abundance per haul of larvae of 10 families with highest relative abundance on *Oceanographer* zig-transect with equivalent coverage on ETP II.

Family	*Oceanographer* (50 stations)			Equivalent ETP II (48 stations)		
	No. positive hauls	Average no. per haul	Rank	No. positive hauls	Average no. per haul	Rank
Myctophidae	50	194.1	1	47	273.9	1
Gonostomatidae	47	87.7	2	45	49.7	2
Clupeidae	2	54.7	3	7	3.9	11
Bathylagidae	47	46.2	4	45	41.8	3
Sternoptychidae	39	19.5	5	40	22.8	5
Engraulidae	6	15.2	6	15	7.9	6
Paralepididae	28	11.1	7	25	6.7	7
Bregmacerotidae	1	9.4	8	9	30.3	4
Carangidae	2	7.1	9	5	1.2	--
Melamphaidae	43	4.9	10	40	5.7	8

tions on ETP II, 5 versus 2 (Table 16), but one of the two positive hauls at *Oceanographer* stations contained 353 larvae. This is considered a chance collection of a patch of larvae. Larvae of Bregmacerotidae were taken in only one *Oceanographer* collection, compared to nine on ETP II. Larvae of two species of *Bregmaceros* were represented in ETP II stations but only larvae of *B. bathymaster* were taken in large numbers. The single *Oceanographer* collection of 470 larvae of this species was made at the inner station off Mexico; two large collections of *B. bathymaster* larvae were made at the two inner stations off Mexico on ETP II (511 and 927 larvae). The principal difference in abundance of *Bregmaceros* larvae between the two coverages appears to be the chance collection of two patches versus one patch of *B. bathymaster* larvae.

I have gone into some detail in order to point up the influence of one or a few larger collections of larvae on the estimates of relative abundance (average number of larvae per haul) of several of the more abundant kinds of larvae in the zig-transect. Larvae of most kinds of fishes are patchily distributed, rather than randomly distributed. Variability associated with patchiness in distribution of larvae may be greater than variability due to temporal changes in reproductive activity. In this comparison, an example of temporal differences in reproductive activity is afforded by the sardine. The exceptionally large collection of thread herring larvae is certainly indicative of very heavy spawning off Mexico in late November; the single larva taken in the same area on ETP II (September 15) may actually be indicative of low reproductive activity or, contrariwise, may simply reflect the circumstance that most hauls of patchily distributed species contain few or no larvae. Striking examples of the influence of one or a few collections on the estimates of abundance of larvae in the two coverages of the zig-transect are afforded by larvae of the two most common species, *Vinciguerria lucetia* (one collection) and *Diogenichthys laternatus* (two collections). I interpret difference in abundance of both species in the two time periods involved to be due primarily to variability associated with patchy distribution of larvae rather than to temporal differences in reproductive activity.

COMMENTS ON LARVAE OF THE MAJOR FISH FAMILIES COLLECTED ON EASTROPAC II

As mentioned in an earlier section, the kinds of larvae obtained on the second multivessel EASTROPAC cruise are summarized in Table 8 by family or larger grouping and by research vessel. This table contains 59 categories: 53 families and 6 composite categories including 3 orders or suborders and those labelled "other identified," "unidentified larvae," and "disintegrated larvae." Only those categories preceded by an asterisk are commented upon in the text discussion that follows; these include 31 families and 4 composite categories. Each category retains the sequential number given to it in this table.

The number of families included in the four composite categories are as follows: other Stomiatoidei (2), Anguilliformes (7), Lophiiformes (10), and "other identified" (10). Hence a total of 82 families were identified from ETP II collections.

Basic data on the kinds and numbers of fish larvae obtained in the 355 ETP II stations are contained in Appendix Tables 1-6, and station data including location, date and time of collection, depth of haul, and standardized haul factors for these stations are given in Appendix Table 8.

TABLE 17.—Comparison of composition of selected families and orders of fish larvae in *Oceanographer* zig-transect versus equivalent ETP II collections.

Categories	*Oceanographer* (50 stations)			Equivalent ETP II coverage (48 stations)		
	No. positive hauls	No. larvae	Average no. per haul	No. positive hauls	No. larvae	Average no. per haul
Clupeidae						
Etrumeus acuminatus	1	6	0.1	3	7	0.1
Opisthonema sp.	1	2,730	54.6	1	1	<0.1
Sardinops sagax	1	1	<0.1	6	177	3.7
Engraulidae						
Engraulis ringens	5	283	5.7	13	378	7.9
Other Engraulidae	1	477	9.5	2	3	0.1
Bathylagidae						
Bathylagus nigrigenys	47	1,315	26.3	45	1,278	26.6
Leuroglossus stilbius urotranus	13	993	19.9	12	727	15.1
Gonostomatidae						
Cyclothone spp.	26	90	1.8	24	75	1.6
Ichthyococcus irregularis	10	19	0.4	12	16	0.3
Maurolicus muelleri	16	177	3.5	12	282	5.9
Vinciguerria lucetia	47	4,085	81.7	45	2,000	41.7
Other Gonostomatidae	8	15	0.3	6	13	0.3
Myctophidae						
Benthosema panamense	1	43	0.9	2	88	1.8
Diaphus spp.	22	57	1.1	11	37	0.8
Diogenichthys laternatus	47	7,314	146.3	43	11,317	235.8
Gonichthys tenuiculus	24	63	1.3	16	52	1.1
Hygophum atratum	6	15	0.3	1	5	0.1
Hygophum proximum	2	2	<0.1	3	3	0.1
Lampanyctus spp.	49	1,041	20.8	38	610	12.7
Myctophum aurolaternatum	19	65	1.3	8	43	0.9
Myctophum nitidulum	27	445	8.9	24	314	6.5
Notolychnus valdiviae	9	24	0.5	10	71	1.5
Notoscopelus resplendens	24	75	1.5	10	80	1.7
Protomyctophum sp.	6	9	0.2	5	10	0.2
Symbolophorus evermanni	20	96	1.9	19	49	1.0
Triphoturus spp.	35	205	4.1	26	321	6.7
Other incl. unidentified myctophids	17	44	0.9	17	73	1.5
Disintegrated myctophids	32	208	4.2	21	76	1.6
Anguilliformes						
Congridae	2	3	0.1	2	3	0.1
Nemichthyidae	3	4	0.1	5	5	0.1
Nettastomidae	1	1	<0.1	0	0	0
Ophichthidae	5	8	0.2	7	11	0.2
Xenocongridae	0	0	0	1	1	<0.1
Family uncertain	2	2	<0.1	2	3	0.1
Lophiiformes						
Caulophrynidae	0	0	0	1	1	<0.1
Ceratiidae	3	3	0.1	1	2	<0.1
Gigantactinidae	1	1	<0.1	2	2	<0.1
Linophrynidae	5	8	0.2	3	3	0.1
Melanocoetidae	7	8	0.2	5	6	0.1
Oneirodidae	5	8	0.2	6	8	0.2
Lophiidae	1	1	<0.1	1	1	<0.1
Family uncertain	7	10	0.2	0	0	0

A summary of these tables follows.

Appendix Table 1.—Counts of fish larvae, tabulated by family, for all stations occupied on EASTROPAC II. This table contains 22 categories including 18 families, 1 suborder, and 3 composite categories for "other identified larvae," "unidentified larvae," and "disintegrated larvae." The latter category includes larvae too damaged or disintegrated to identify with any certainty.

Appendix Table 2.—Counts of myctophid larvae, tabulated by genus or species, for all stations occupied on the second multivessel EASTROPAC cruise (ETP II). Myctophid larvae are tabulated by species for 13 kinds, by genus for 6 kinds, and 3 composite categories—"other

identified myctophids," "unidentified myctophids," and "disintegrated myctophids." A summary of this appendix table is contained in Table 19.

Appendix Table 3.—Counts of selected categories of fish larvae, tabulated by station, for all stations occupied on ETP II. Table contains 23 categories including 11 species, 5 genera, and 7 families. Of these, 12 were included in the category "other identified larvae" in Appendix Table 1, the remainder provide information on counts of larvae at the generic or specific level for several families listed in Appendix Table 1.

Appendix Table 4.—Summary of occurrences and numbers of larvae of 23 categories, limited in distribution to a broad coastal band or around offshore islands or banks. Only positive stations are included. These 23 categories were included under "other identified larvae" in Appendix Table 1.

Appendix Table 5.—Numbers and kinds of eel leptocephali (Anguilliformes) obtained on the second multivessel EASTROPAC cruise (ETP II), tabulated by family for all positive hauls. A summary of this table is given in Table 20.

Appendix Table 6.—Numbers and kinds of lophiiform larvae obtained on the second multivessel EASTROPAC cruise (ETP II) tabulated by family for all positive hauls. A summary of this table is given in Table 23.

Appendix Table 7.—7A contains counts of fish larvae, tabulated by family or larger grouping, for all stations occupied by *Oceanographer* on zig-transect; 7B contains station counts of myctophid larvae for same cruise, tabulated by genus or species; and 7C contains station counts of selected categories of fish larvae on same cruise.

Appendix Table 8.—Station data and standardized haul factors for second multivessel EASTROPAC cruise and for *Oceanographer* zig-transect. Included for each station are locality, date and time of collection, depth of haul, and standardized haul factor. The standardized haul factors are used to adjust original counts of larvae to the comparable standard of numbers of larvae in 10 m^3 of water strained per meter of depth fished. It should be noted that the mid-time of haul for each station is recorded as Pacific Standard Time. However, the symbols D (Daylight), N (Night), DT (Day Twilight), NT (Night Twilight) accurately reflect the local condition at each station. Twilight hauls were taken within 1 hr of local sunrise or sunset.

2. CLUPEIDAE
(9 occurrences, 270 larvae)

As on ETP I, three species of Clupeidae larvae were obtained. Larvae of the sardine, *Sardinops sagax* (Jenyns), (7 occurrences, 179 larvae) and round herring, *Etrumeus acuminatus* Gilbert, (3 occurrences, 7 larvae) were taken in the vicinity of the Galapagos Islands while larvae of the thread herring, *Opisthonema* sp., (2 occurrences, 84 larvae) were taken at two coastal stations off southern Mexico, with surface water temperatures of 28.7° and 29.3°C. Six of the occurrences of sardine larvae were at contiguous stations, along long 92°W, between lat 1°N and 3°S, just seaward of the Galapagos Islands (Figure 3). Surface water temperatures at these stations ranged between 16.4° and 19.3°C. We sampled the Galapagos sardine population on ETP II, at a period of rather high reproductive activity.

3. ENGRAULIDAE
(35 occurrences, 1,360 larvae)

The Peruvian anchovy, *Engraulis ringens* Jenyns, (25 occurrences, 1,307 larvae) also was sampled on ETP II during a period of high reproductive activity (Figure 3). Einarsson and Rojas de Mendiola (1967) determined that the spawning season of the Peruvian anchovy extended from August to March, hence the early part of the 1967-68 spawning season was sampled on ETP II and the close of the previous spawning season on ETP I. Surface temperatures at positive stations ranged between 15.4° and 18.8°C. Larvae of other engraulids (10 occurrences, 53 larvae) were taken at nearshore stations over a wide area between lat 20°N and the equator.

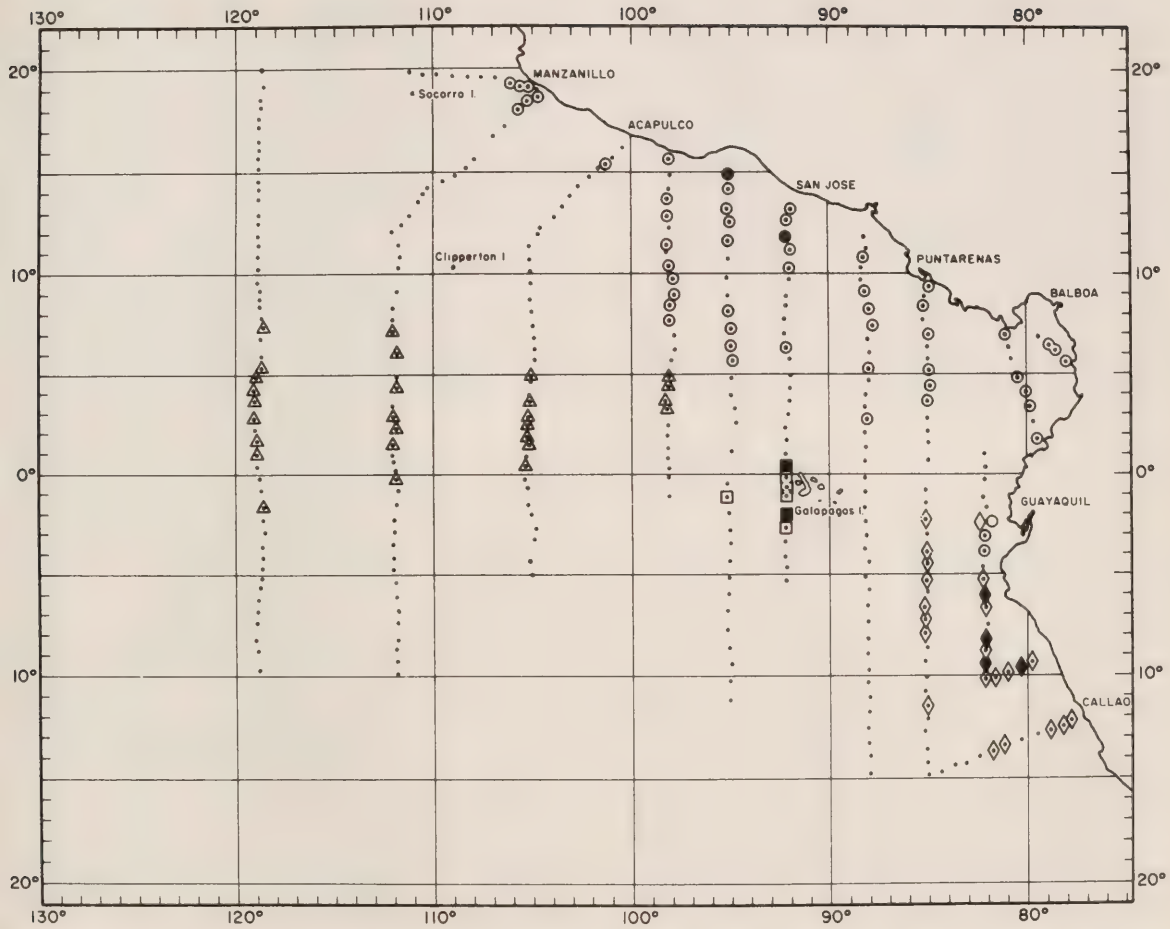

FIGURE 3.—Distribution of larvae of the clupeid, *Sardinops sagax* (open square with dot, 1-50 larvae; closed square, 51 or more larvae), of the engraulid, *Engraulis ringens* (open diamond with dot, 1-100 larvae; closed diamond, 101 or more larvae), of the myctophid, *Myctophum asperum* (open triangle with dot), and of the bothid flatfish, *Syacium ovale* (open circle with dot, 1-100 larvae; large solid circles, 101 or more larvae). Small solid circles represent other stations occupied on ETP II.

4. ARGENTINIDAE
(32 occurrences, 58 larvae)

In contrast to ETP I, from which three kinds of argentinid larvae were obtained, only one kind, *Nansenia* sp. A, was obtained on ETP II. Larvae of *Nansenia* were taken in an offshore equatorial band, between lat 8°N and 7°S. This distribution is closely similar to that illustrated for ETP I (Ahlstrom, 1971, Figure 2).

5. BATHYLAGIDAE
(298 occurrences, 5,891 larvae)

Larvae of two species of bathylagid smelts were taken on ETP II: *Bathylagus nigrigenys* Parr (293 occurrences, 3,787 larvae) and *Leuroglossus stilbius urotranus* (Bussing) (29 occurrences, 2,104 larvae).

In comparable coverage on ETP I, 2,852 larvae of *B. nigrigenys* were taken in 269 collections. The distribution of larvae on the two coverages was strikingly similar (Ahlstrom, 1971, Figure 3). On the two outer lines, occu-

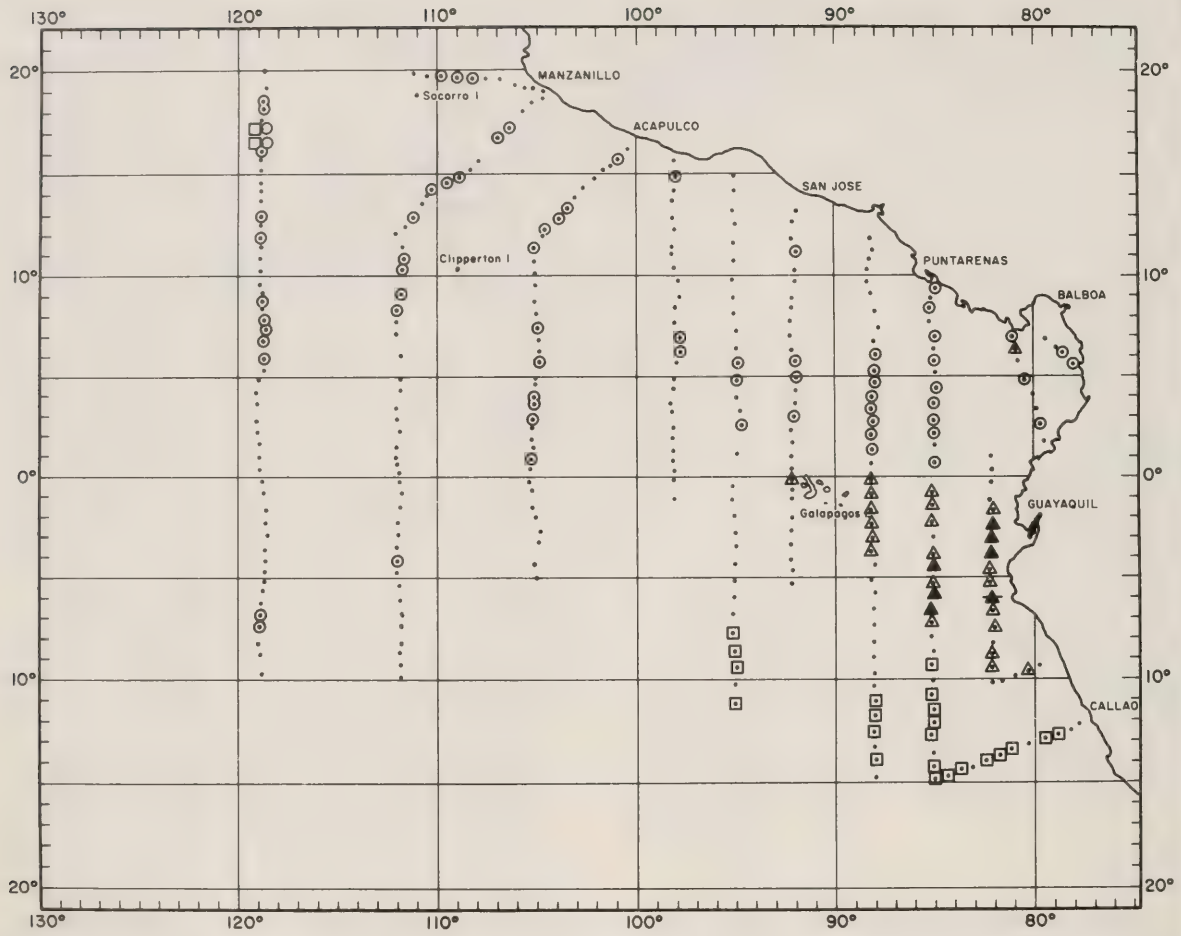

FIGURE 4.—Distribution of larvae of the bathylagid, *Leuroglossus stilbius urotranus* (open triangle with dot, 1-100 larvae; closed triangle, 101-500 larvae, and triangle with bisecting line, 501 or more), of the gempylid, *Gempylus serpens* (open circle with dot), and of the trichiurid, *Diplospinus multistriatus* (open square with dot). Small solid circles represent other stations occupied on ETP II.

pied by *Washington*, no larvae of *B. nigrigenys* were taken below ca. lat. 4°S. Absence of larvae of this species from the South Pacific central water mass was not as conclusively documented as on ETP I, primarily because of the paucity of coverage within the central water mass on ETP II. Counts of larvae exceeded 100 specimens per haul in five samples, taken between 0° and lat 3°S and long 85° to 92°W.

Larvae of *Leuroglossus stilbius urotranus* were taken in 29 collections; all but 2 of which were obtained in a compact area shoreward of the Galapagos Islands between 0° and lat 10°S (Figure 4). The distribution of larvae of this species is one of the few that shows a striking contrast between ETP I and ETP II. On ETP I about half of the occurrences were to the north of the equator between 0° and lat 8°N (18 occurrences, 218 larvae—Ahlstrom, 1971, Figure 2), compared with only one occurrence, one larva in this area on ETP II. The distribution south of the equator was essentially similar on both surveys; on ETP I, 1,672 larvae were taken in 19 collections between 0° and lat 14°S, with the heaviest concentration of larvae in hauls taken between lat 3° and 6°S.

6. GONOSTOMATIDAE
(342 occurrences, 24,255 larvae)

Gonostomatid larvae, exceeded in abundance only by myctophid larvae, were obtained in 97% of the ETP II collections and contributed 19.7% of the total fish larvae. The relative abundance and frequency of occurrences of larvae belonging to 10 genera of gonostomatids are summarized by vessel patterns in Table 18. The last two columns of this table give information concerning occurrence and relative abundance of gonostomatid larvae of the same genera for comparable coverage on ETP I.

Little change in abundance, distribution, or frequency of occurrence was shown by larvae of *Cyclothone* spp. and *Diplophos taenia* Günther, although both were slightly more abundant on ETP I. Average abundance of larvae of *Vinciguerria* spp. was about one-third greater than on equivalent ETP I, and almost three times as many larvae of *Maurolicus muelleri* (Gmelin) were obtained on ETP II. An interesting instance of a marked difference in seasonal abundance of larvae of a gonostomatid fish was found for larvae of *Yarrella argenteola* (Garman). Larvae of this species were taken in 17 collections on ETP II (Figure 6), whereas only one specimen was obtained on ETP I.

Araiophos eastropas Ahlstrom and Moser
(1 occurrence, 35 larvae)

The single record on ETP II is from the southernmost station occupied by *Washington* on its outer line at lat 9°45'S, long 118°59'W. On ETP I, all occurrences of larvae of this species were taken between lat 10° and 18°S along long 119° and 126°W (Ahlstrom, 1971, Figure 4). Hence, it was exciting to obtain the single ETP II collection of larvae of *Araiophos* at the only station in the pattern that bordered on the distributional limits of this species as determined from ETP I collections.

Cyclothone spp.
(187 occurrences, 972 larvae)

Larvae of *Cyclothone* spp. were taken in about an equal number of collections in the two surveys, 187 on ETP II versus 190 on equivalent coverage of ETP I, and in rather similar abundance—2.7 larvae per haul on ETP II as compared with 3.1 on equivalent ETP I. The distribution of larvae of *Cyclothone* on ETP II was similar to that illustrated for equivalent ETP I. As on ETP I, the fewest occurrences (19 of 68 collections) were obtained between lat 10° and 20°N, and the Peruvian coastal waters were almost as poor. However, *Cyclothone* larvae were more abundant in the portion of ETP I that was

TABLE 18.—Frequency of occurrence and relative abundance of the kinds of gonostomatid larvae on EASTROPAC II, and for equivalent coverage on EASTROPAC I.

Gonostomatid genera or species	*Washington* 45.000 series		*Undaunted* 46.000 series		*Rockaway* 47.000 series		EASTROPAC II total (355 hauls)		Equivalent EASTROPAC I total (355 hauls)	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
Araiophos eastropas	1	35	0	0	0	0	1	35	0	0
Cyclothone spp.	64	358	54	331	69	283	187	972	190	1,106
Danaphos oculatus	1	1	0	0	0	0	1	1	0	0
Diplophos taenia	44	114	11	20	2	2	57	136	57	156
Gonostoma spp.	2	3	1	1	8	18	11	22	10	39
Ichthyococcus sp.	3	3	25	38	18	35	46	76	34	53
Maurolicus muelleri	4	11	24	551	19	211	47	773	43	264
Vinciguerria spp.	107	8,553	94	6,148	140	7,497	341	22,198	320	16,746
Woodsia sp.	0	0	2	3	2	2	4	5	3	3
Yarrella argenteola	0	0	1	1	17	32	18	33	1	1
Other gonostomatids	1	1	2	2	1	1	4	4	12	12
Total gonostomatids	108	9,079	94	7,095	140	8,081	342	24,255	333	18,380

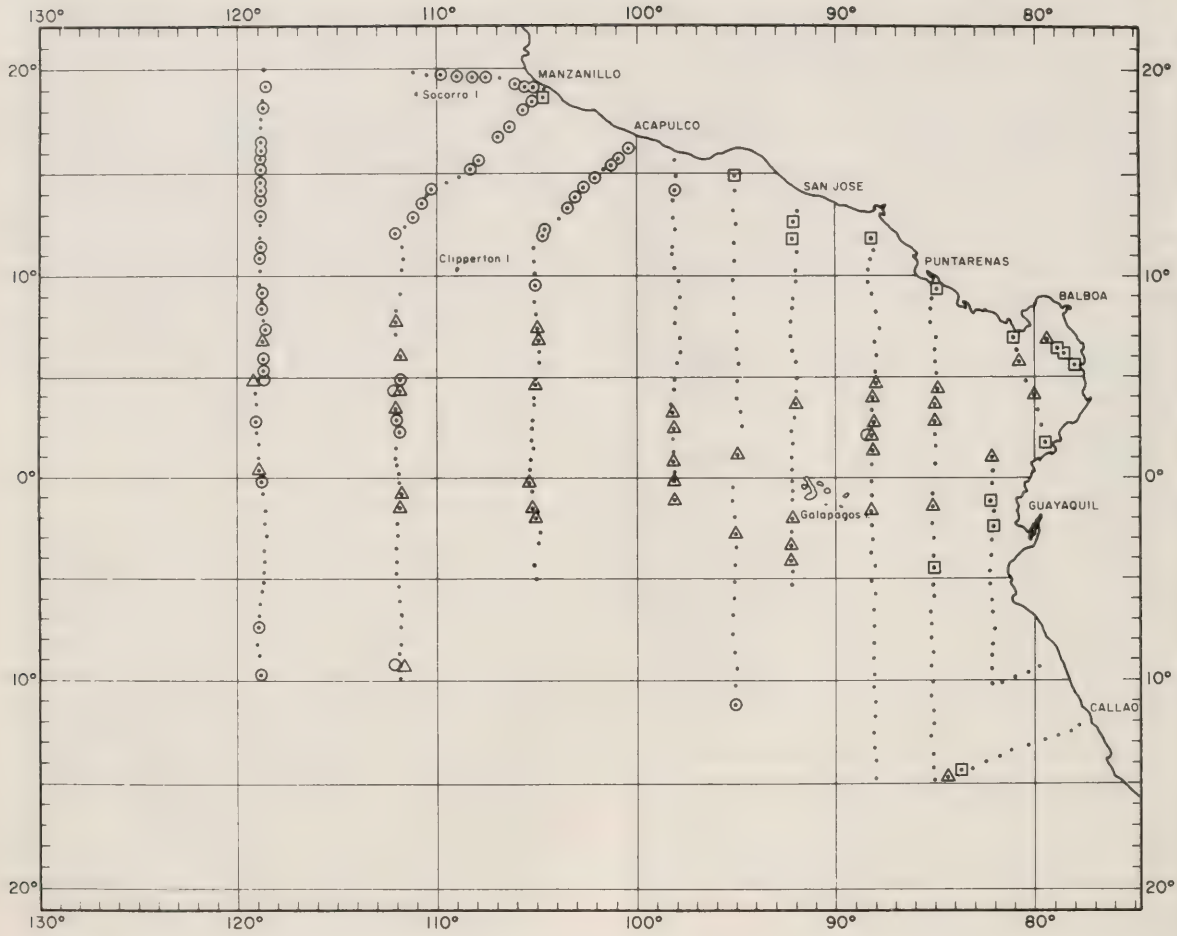

FIGURE 5.—Distribution of larvae of the gonostomatid, *Diplophos taenia* (open circle with dot), of the stomiatoid family, Astronesthidae (open triangle with dot), and of the synodontid genus, *Synodus* spp. (open square with dot). Small solid circles represent other stations occupied on ETP II.

not replicated on ETP II. In these collections *Cyclothone* larvae occurred in 111 of 127 collections, with an average abundance per collection of 8.7 larvae.

Danaphos oculatus (Garman)
(1 occurrence, 1 larva)

A single large larva was taken at the northern end of the *Washington* pattern at lat 19°16'N, long 118°56'W. Information obtained from California Current and NORPAC collections indicates that *Danaphos* is a temperate water species, occurring most commonly in collections obtained from the central water mass of the North Pacific in hauls which sampled to depths greater than 140 m.

Diplophos taenia (Günther)
(57 occurrences, 136 larvae)

Larvae of *Diplophos taenia* afford a striking example of similarities in distribution, frequency of occurrences, and relative abundance in the

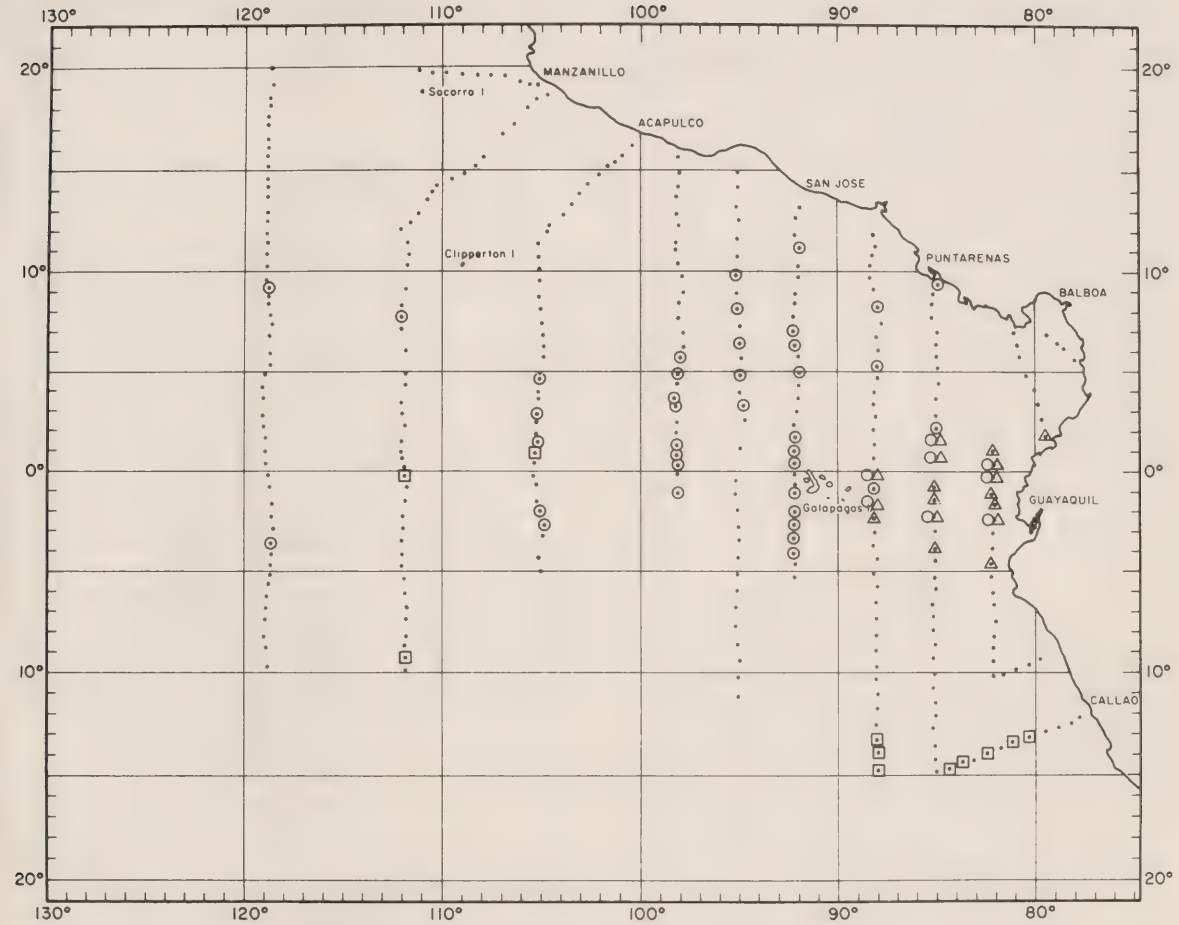

FIGURE 6.—Distribution of larvae of three kinds of gonostomatids. Records of occurrence of larvae of *Gonostoma* spp. shown as open square with dot, of *Ichthyococcus irregularis* as open circle with dot, and of *Yarrella argenteola* as open triangle with dot. Small solid circles represent other stations occupied on ETP II.

two EASTROPAC multivessel cruises. Larvae were obtained in 57 collections from both ETP II and equivalent ETP I; on both surveys the majority of larvae were taken to the north of lat 10°N, particularly on the coastward-oriented portion of the station line terminating off Acapulco, Mexico, and that terminating off Manzanillo, Mexico (Figure 5, and Ahlstrom, 1971, Figure 4). Larvae of this species were taken in moderate numbers, seldom more than 5 per haul; the average number per haul on ETP II was 0.38 larva versus 0.44 larva on equivalent ETP I.

***Gonostoma* sp.**
(11 occurrences, 22 larvae)

At least two kinds of gonostomatid larvae have been referred to *Gonostoma*, the more common being larvae of *G. elongatum* Günther. The distribution of *Gonostoma* larvae on ETP II is shown in Figure 6; 8 of 11 occurrences were in a compact group in the southern, inshore portion of the ETP pattern (between lat 13° and 15°S, offshore to long 88°W).

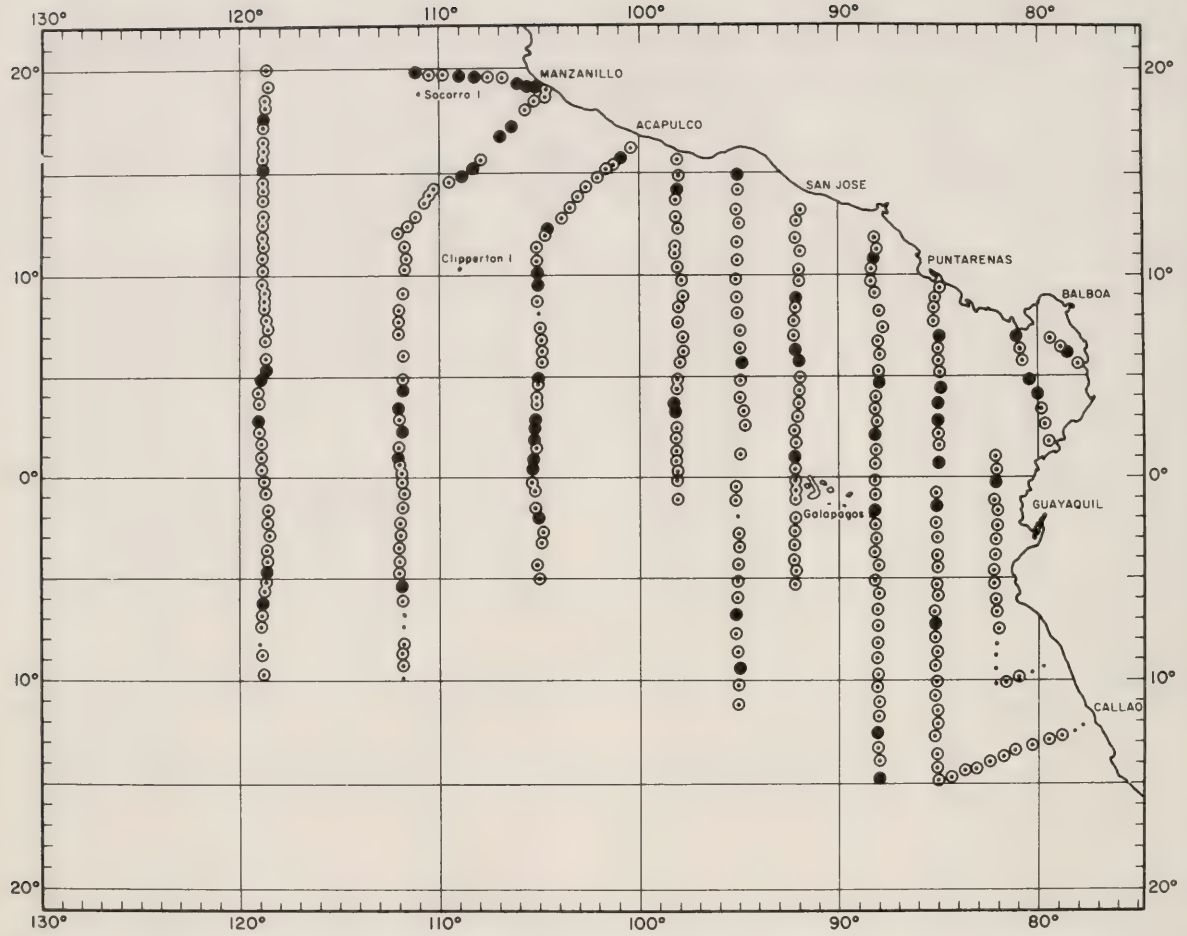

FIGURE 7.—Distribution of larvae of the gonostomatid, *Vinciguerria* spp. on ETP II. Collections of 1-100 larvae are shown as open circles with dot in center, collections of 101 or more larvae as large solid circles; negative hauls are shown as small solid circles.

Ichthyococcus sp.
(46 occurrences, 76 larvae)

All *Ichthyococcus* larvae taken on ETP II were similar in appearance and have been referred to *I. irregularis* Rechnitzer and Böhlke. Although widely distributed (Figure 6), all larvae were obtained between lat 12°N and 4°S; only three collections of *Ichthyococcus* larvae were taken in the outer pattern occupied by *Washington*.

Maurolicus muelleri (Gmelin)
(47 occurrences, 773 larvae)

Larvae of *M. muelleri* ranked third in abundance among gonostomatid larvae. As on ETP I, (Ahlstrom, 1971, Figure 4) larvae of this species were sampled in a rather narrow equatorial belt, and none were taken seaward of long 112°W. This again is a striking instance of the similarity in distribution of larvae on the two multivessel cruises. Although the incidence of occurrences of *Maurolicus* larvae was almost as

high in ETP I as in ETP II, 43 positive hauls as compared with 47, the average number of larvae per positive haul was much higher on ETP II—16.4 larvae versus 6.1 larvae.

Vinciguerria spp.
(341 occurrences, 22,198 larvae)

As in ETP I, larvae of *Vinciguerria* spp. ranked second in overall abundance, exceeded only by larvae of the myctophid, *Diogenichthys laternatus* (Garman). They were obtained throughout the EASTROPAC pattern, occurring in 96% of the collections (Figure 7). Average abundance of larvae per haul was about one-third greater than in ETP I: 62.5 versus 47.2 larvae.

Larvae of two species of *Vinciguerria* occur within the ETP II pattern, although most were those of *V. lucetia* Garman. As commented upon for ETP I, larvae of *V. nimbaria* (Jordan and Williamson) were taken principally in the South Pacific central water mass, to the south of about lat 5°S. On ETP II this distribution involves about 20 collections only.

Yarrella argenteola (Garman)
(18 occurrences, 33 larvae)

Larvae of *Y. argenteola* were taken in a limited area shoreward or immediately south of the Galapagos Islands between lat 2°N and 5°S (Figure 6). No metamorphosing specimens were observed, although larvae as large as 16 mm were represented in the collections. As noted in the introductory section, only one specimen of *Yarrella* was obtained on ETP I, in contrast to the 18 occurrences on ETP II. Adults of this species were recorded from within the area covered on ETP II by Morrow (1957b), Grey (1960), Bussing (1965), and Parin (1971).

7. STERNOPTYCHIDAE
(277 occurrences, 7,385 larvae)

As in ETP I, hatchetfish larvae ranked third in abundance. Although hatchetfish larvae contributed almost identical percentages of the total larvae in ETP II as in comparable ETP I (5.99% versus 5.98%), the average number of larvae per haul, 20.8 versus 13.9, reflected the greater relative abundance of larvae on ETP II. As noted for ETP I, hatchetfish larvae are more fragile than most kinds, and a portion of the larvae are too damaged to identify, except to family. Even so, identification to genus was made for most ETP II collections, and in these, larvae of *Sternoptyx* sp. contributed about 85% of the total and larvae of *Argyropelecus* (mostly *A. lychnus* Garman), the remainder. Baird (1971) in his revision of the family Sternoptychidae recognized three species of *Sternoptyx*, with *S. obscura* Garman the common species in the eastern tropical Pacific; however, he included one record of *S. diaphana* Hermann from within the area surveyed on ETP II.

8. ASTRONESTHIDAE
(42 occurrences, 74 larvae)

Astronesthid larvae were taken in about four times as many collections as on equivalent ETP I. Most larvae had an equatorial distribution between lat 8°N and 5°S; only two larvae occurred elsewhere (Figure 5). Three distinctive kinds of astronesthid larvae were taken.

9. CHAULIODONTIDAE
(56 occurrences, 207 larvae)

Although larvae of *Chauliodus* sp. were taken in a comparable number of hauls on ETP II and ETP I (56 versus 59 occurrences), more larvae were obtained on ETP II (207 versus 134 larvae). The majority of *Chauliodus* larvae on ETP II were taken in the inner half of the ETP pattern, below the equator—34 collections containing 165 specimens were obtained from this quadrant (Figure 8). In other parts of the ETP pattern somewhat fewer larvae were taken than on ETP I. As on ETP I, the majority of positive hauls contained 1 to 3 larvae (41 of 56 hauls); even so, a higher proportion of the hauls on ETP II contained somewhat larger numbers of *Chauliodus* larvae, i.e., 6 to 26 larvae per haul.

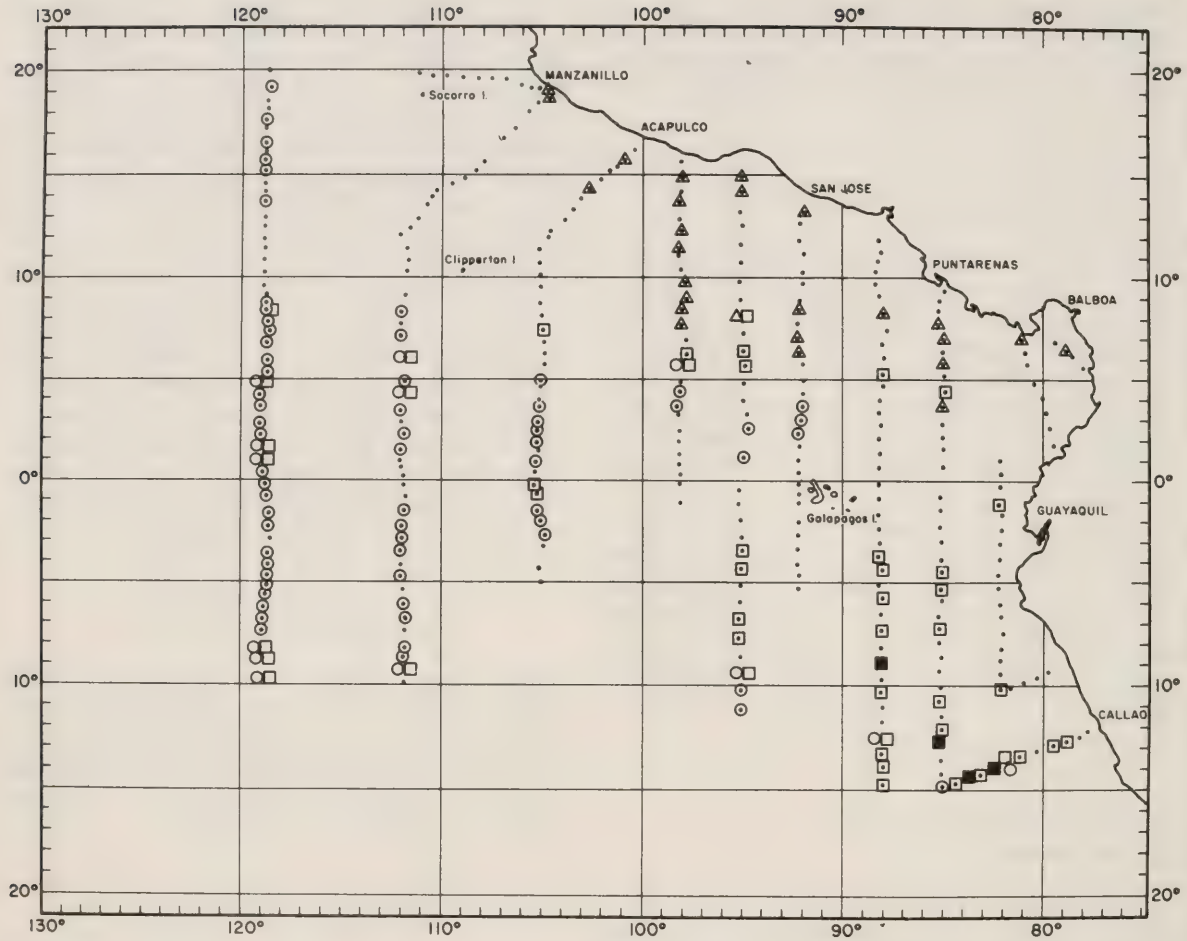

FIGURE 8.—Distribution of larvae of the stomiatoid genus *Chauliodus* sp. (open square with dot, 1-10 larvae, closed square, 11 or more larvae), of the myctophid, *Hygophum proximum* (open circle with dot), and of the bothid flatfish, *Bothus leopardinus* (open triangle with dot). Small solid circles represent other stations occupied on ETP II.

10. IDIACANTHIDAE
(181 occurrences, 795 larvae)

Larvae of *Idiacanthus* sp. were taken in over half of the plankton hauls made on ETP II; there was an increase in frequency of occurrence of *Idiacanthus* larvae as compared to equivalent ETP I, but not in actual abundance of larvae. Larvae of *Idiacanthus* were most abundant in the inshore quadrant to the north of the equator and least abundant in the offshore quadrant south of the equator (Figure 9). All larger collections of larvae (11 to 43 larvae per haul) were taken to the north of the equator, usually within 600 miles of the coast.

11. OTHER STOMIATOIDEI
(210 occurrences, 1,034 larvae)

Included under other Stomiatoidei in Table 9 are larvae of two stomiatoid families: Stomiatidae and Melanostomiatidae. In Appendix Table 1, the category "other Stomiatoidei" also includes the family Astronesthidae. In Appendix Table 3, counts are given for three principal

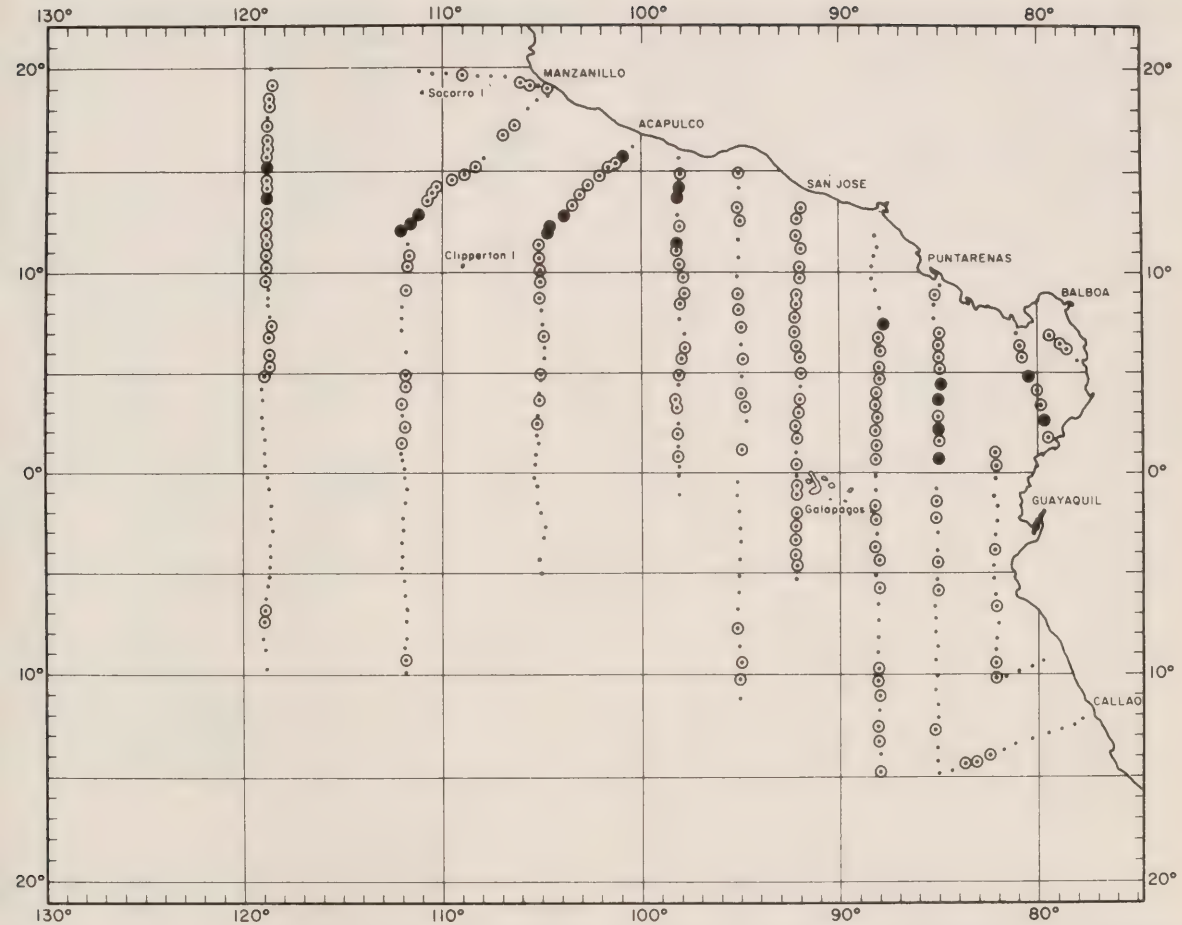

FIGURE 9.—Distribution of larvae of the stomiatoid genus *Idiacanthus* sp. on ETP II. Collections of 1-10 larvae are shown as open circles with dot in center, collections of 11 or more larvae as large solid circles; negative hauls are shown as small solid circles.

constituents: Astronesthidae, *Bathophilus filifer* (Garman), and *Stomias* sp.

Stomias larvae (43 occurrences, 177 larvae) were most abundant in the inner pattern. Larvae of three categories of Melanostomiatidae were identified to the genus or species level. The most common of these were larvae of *Bathophilus filifer* (Garman) (104 occurrences, 310 larvae). Larvae of *Eustomias* spp. (10 occurrences, 19 larvae) represented several species, whereas larvae of *Leptostomias* sp. (8 occurrences, 17 larvae) were those of a single species.

Approximately half of the stomiatoid larvae (140 occurrences, 511 larvae) were not identified below the subordinal level. These were mostly small or damaged specimens; some of the unidentified stomiatoid larvae possibly are those of Malacosteidae.

13. EVERMANNELLIDAE
(17 occurrences, 67 larvae)

The majority of evermannellid larvae were

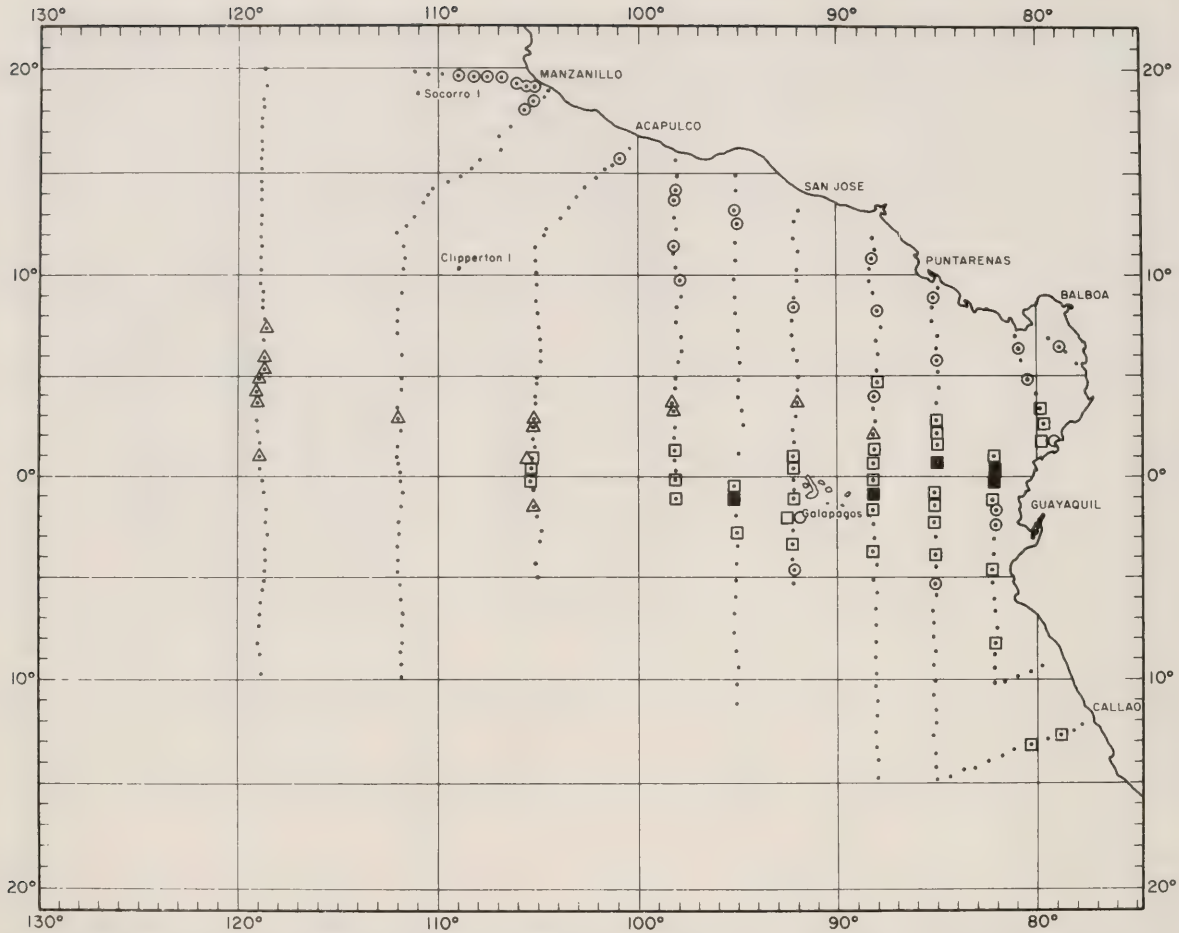

FIGURE 10.—Distribution of larvae of the myctophiform families Evermannellidae (open triangle with dot), and Scopelosauridae (open squares with dot, 1-25 larvae, closed squares, 26 or more larvae) and of the perciform family, Labridae (open circle with dot); negative hauls are shown as small solid circles.

taken on the outer line of stations along long 119°W; the remainder were taken in an equatorial band between lat 2°S and 4°N (Figure 10). This distribution is less widespread than that encountered on ETP I; however, 17 of the records of occurrence on ETP I were in the southern portion of the pattern not covered on ETP II.

14. MYCTOPHIDAE
(352 occurrences, 64,009 larvae)

Larvae of Myctophidae were more abundant on ETP II than on ETP I; the increase in abundance of myctophid larvae per haul in ETP II over ETP I was 1.63×. Much of the increase was due to the greater abundance of larvae of the dominant species, *Diogenichthys laternatus* (Garman), although a number of kinds of myctophid larvae were taken in somewhat greater abundance, and only a few kinds were taken in lesser numbers per haul (Table 19). To show changes in relative abundance of myctophid larvae between the two multivessel cruises, I have arranged the more common kinds in order of their relative abundance on ETP II as compared

TABLE 19.—Frequency of occurrence and relative abundance of the kinds of myctophid larvae on EASTROPAC II, and for equivalent coverage on EASTROPAC I.

Myctophid genera or species	*Washington* 45.000 series		*Undaunted* 46,000 series		*Rockaway* 47.000 series		EASTROPAC II total		Equivalent EASTROPAC I total	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
* *Benthosema panamense*	3	72	2	88	8	971	13	1,131	7	1,027
Benthosema suborbitale	1	1	1	1	0	0	2	2	7	7
Centrobranchus sp.	1	2	0	0	0	0	1	2	0	0
* *Ceratoscopelus townsendi* complex	12	365	0	0	1	24	13	389	37	349
* *Diaphus* spp.	73	938	53	1,113	51	382	177	2,433	168	1,931
* *Diogenichthys atlanticus*	1	1	0	0	3	9	4	10	6	7
* *Diogenichthys laternatus*	92	4,661	90	16,440	138	25,865	320	46,966	302	24,315
Diogenichthys sp.	0	0	0	0	2	4	2	4	0	0
* *Gonichthys tenuiculus*	15	25	27	99	64	169	106	293	88	226
* *Hygophum atratum*	38	335	10	46	18	140	66	521	85	629
* *Hygophum proximum*	54	499	15	75	8	50	77	624	55	448
* *Lampadena* spp.	7	8	3	6	0	0	10	14	15	27
Lampanyctus spp.	84	1,013	72	1,629	135	2,692	291	5,334	271	5,262
* *Lepidophanes pyrsobolus* complex	16	53	12	73	8	12	36	138	13	41
* *Lobianchia* sp.	5	8	2	2	3	5	10	15	10	26
* *Loweina laurae*	10	15	10	14	5	8	25	37	31	41
* *Myctophum aurolaternatum*	37	85	41	144	70	445	148	674	145	529
* *Myctophum asperum*	16	118	10	62	0	0	26	180	(1)	(1)
* *Myctophum nitidulum*	25	300	43	274	66	717	134	1,291	(1)	(1)
* *Myctophum* other	11	27	6	13	0	0	17	40	117	1,042
* *Notolychnus valdiviae*	36	147	31	247	33	140	100	534	106	605
* *Notoscopelus resplendens*	14	28	29	198	35	156	78	382	54	231
* *Protomyctophum* sp.	5	7	12	22	8	15	25	44	33	74
* *Symbolophorus evermanni*	43	248	38	140	74	434	155	822	132	906
* *Triphoturus* spp.	23	40	27	132	94	652	144	824	111	356
Unidentified myctophid larvae	33	86	33	94	50	217	116	397	115	295
Disintegrated myctophid larvae	79	464	42	170	84	274	205	908	155	876
Total myctophid larvae	111	9,546	95	21,082	146	33,381	352	64,009	346	39,249

[1] Not separately tabulated.

to ETP I (comparable coverage, identical number of samples).

Genus or species of myctophid	*No. in ETP II* / *No. in ETP I*
Hygophum atratum-reinhardti	0.83
Notolynchus valdiviae	0.88
Symbolophorus evermanni	0.91
Lampanyctus spp.	1.01
Benthosema panamense	1.10
Ceratoscopelus townsendi-complex	1.11
Diaphus spp.	1.26
Myctophum aurolaternatum	1.27
Gonichthys tenuiculus	1.30
Hygophum proximum	1.39
Myctophum spp. (other than *M. aurolaternatum*)	1.45
Notoscopelus resplendens	1.66
Diogenichthys laternatus	1.93
Triphoturus spp.	2.31

Benthosema panamense **(Tåning)**
(13 occurrences, 1,131 larvae)

Although larvae of this species ranked fifth in abundance among myctophid larvae, they were collected in a relatively narrow coastal band, no wider than 200 miles (Figure 11). A similar pattern of inshore, clumped distribution was encountered on ETP I (Moser and Ahlstrom, 1970, Figure 45).

Benthosema suborbitale **(Gilbert)**
(2 occurrences, 2 larvae)

Only two specimens of the larvae of *Benthosema suborbitale* were taken on ETP II. Larvae of this species only recently have been positively identified. The larval series was initially established by Dr. H. G. Moser from *Dana* material. Larvae are strikingly similar to *Electrona*

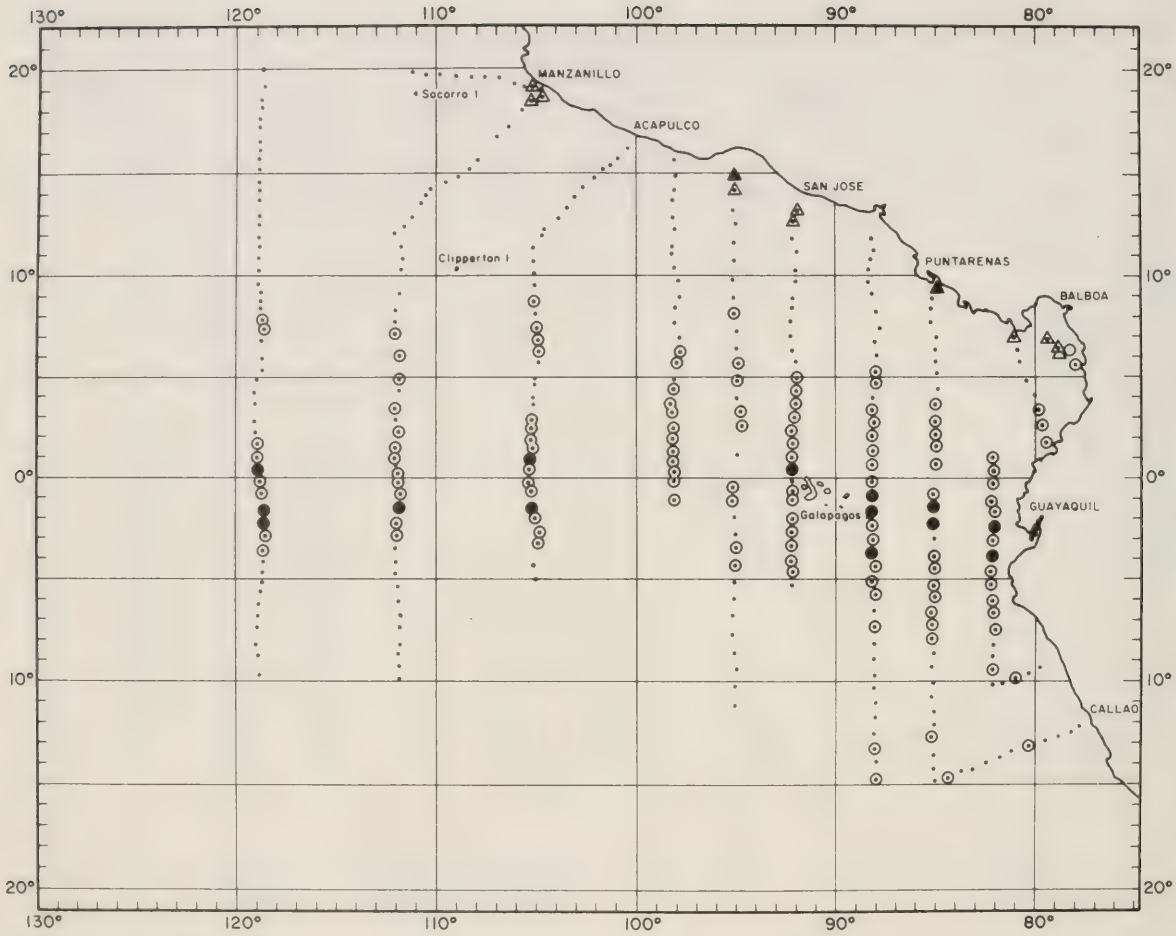

FIGURE 11.—Distribution of larvae of two species of myctophid lanternfishes. Records of occurrence of larvae of *Benthosema panamense* are shown as open triangles with dot for collections of 1-100 larvae, and as closed triangles for collections containing 101 or more larvae; records of occurrence of larvae of *Myctophum nitidulum* are shown as open circles with dot for collections of 1-25 larvae, and as large solid circles for collections containing 26 or more larvae; negative hauls are shown as small solid circles.

larvae, and earlier were confused with larvae of this genus. Most larvae included in *Electrona* sp. in the ETP I compilation were those of this species. The majority of occurrences of the larvae of this species on ETP I was in the southern, offshore portion of the ETP pattern, not covered on ETP II.

Ceratoscopelus townsendi-complex (13 occurrences, 389 larvae)

Abbreviated coverage of the southern portion of the EASTROPAC pattern, with coverage limited to lat 10°S or 5°S on offshore lines, cut down markedly on the occurrences of larvae of *Ceratoscopelus*, as compared with ETP I: 13 occurrences as compared with 110. All occurrences but one of *Ceratoscopelus* larvae on ETP II were obtained in the outer pattern, occupied by *Washington*: 2 at the two northernmost stations along long 119°W, and 10 in the southern portion of the pattern between lat 6° and 10°S along long 119° and 112°W (Figure 12). Both clus-

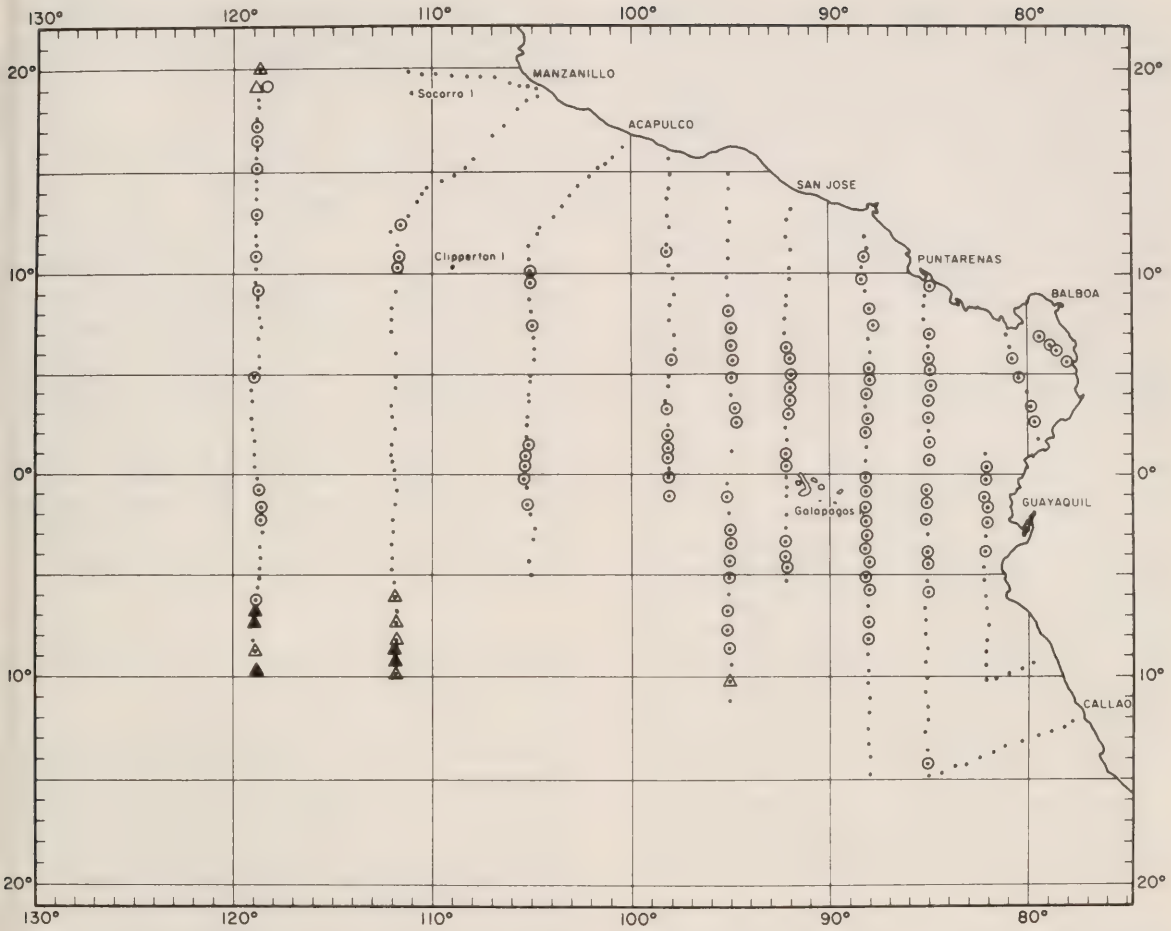

FIGURE 12.—Distribution of larvae of two species of myctophid lanternfishes. Records of occurrence of larvae of *Ceratoscopelus townsendi*-complex are shown as open triangles with dot for collections of 1-25 larvae and as closed triangles for collections of 26 or more larvae; records of occurrence of larvae of *Gonichthys tenuiculus* are shown as open circles with dot; negative hauls are shown as small solid circles.

ters of larvae occurred in the central water masses of the North and South Pacific.

Diaphus spp.
(177 occurrences, 2,433 larvae)

Larvae of *Diaphus* rank third in abundance among myctophid genera, exceeded only by *Diogenichthys* and *Lampanyctus*. Although *Diaphus* larvae were taken in half the collections made on ETP II, occurrences and nonoccurrences tended to be clustered. Almost two-thirds of *Diaphus* larvae were obtained to the north of lat 10°N on the four outer station lines; these were predominantly larvae of *D. pacificus* Parr. The largest area of nonoccurrence was off Peru, between lat 5° and 15°S; here *Diaphus* larvae were absent from 42 consecutive stations, 47.081 to 47.197. Larvae of the subgenus *Diaphus*, which are quite distinctive, made up about 10% of the total.

Juveniles and adult *Diaphus*, separated from micronekton hauls made on ETP I, have been identified, with the cooperation of Robert Wisner of Scripps Institution of Oceanography: 15 species were represented in the collection made by *Argo*, *David Starr Jordan*, and *Alaminos* on ETP I. *D. pacificus* was, by far, the most abundant species, occurring in more collections and in larger numbers than other species of *Diaphus*. This species occurs in a broad coastal belt, 600 to 800 miles wide, from lat 20°N to the vicinity of the equator. Six species were taken offshore, between lat 5° and 20°S, in the South Pacific central water mass, including *D. rolfbolini* Wisner, *D. brachycephalus* Tåning, *D. fragilis* Tåning, *D. jenseni* Tåning, *D. schmidt* Tåning, and *D. splendidus* (Brauer). Five species were taken in an offshore equatorial belt, between lat 10°N and 5°S, including *D. garmani* Gilbert, *D. malayanus* Weber, *D. termophilus* Tåning, *D. lucidus* Goode and Bean, and *D. lutkeni* Brauer, the latter showing some admixture with central water mass species. Species belonging to subgenus *Diaphus*, tentatively identified by Wisner as *D. longleyi* Fowler and *D. mollis-nanus* complex had quite widespread distributions.

Now that the species composition of adult *Diaphus* has been clarified, life history series can be determined for the more common kinds.

Diogenichthys laternatus (Garman) (320 occurrences, 46,966 larvae)

Larvae of *D. laternatus* were outstandingly abundant, making up 38.1% of the total fish larvae obtained on ETP II. Almost twice as many *D. laternatus* larvae were taken in equivalent coverage of the EASTROPAC region on ETP II as on ETP I; 46,966 versus 24,315 larvae. The number of collections that contained *D. laternatus* larvae, however, was not much different: 302 of 355 in ETP I as compared with 320 of 355 in ETP II. Almost one collection in three from ETP II contained over 100 *D. laternatus* larvae, and 19 collections contained over 500 larvae. Of these larger collections, 13 of 19 were taken between lat 5° and 10°N. As on ETP I, larvae of *D. laternatus* were *not* taken in collections made within the central water mass of the South Pacific (Figure 13).

Diogenichthys atlanticus (Tåning) (4 occurrences, 10 larvae)

Larvae of this species were taken more frequently on ETP I (29 occurrences, 92 larvae); however, all but six of these occurrences were in the portion of the ETP I pattern that was not covered on ETP II. The four records on ETP II were taken between lat 9° and 15°S, with two occurrences in the transitional waters of the Humboldt Current and only one occurrence offshore in the central water mass. Larvae of this species were commonly taken on MARCHILE VI off Chile (12 occurrences, 100 + larvae).

Gonichthys tenuiculus (Garman) (106 occurrences, 293 larvae)

Larvae of *Gonichthys* had rather similar distributions and frequency of occurrences in the two multivessel EASTROPAC surveys. The majority of larvae were obtained in the inner pattern occupied by *Rockaway*, with highest frequency of occurrences in an equatorial belt between lat 5°N and 5°S (Figure 12).

Hygophum atratum (Garman) (66 occurrences, 521 larvae)

The less extensive coverage on ETP II eliminated the area in which *H. reinhardti* (Lütken) larvae were taken on ETP I, and only larvae of *H. atratum* were observed in ETP II collections. Larvae of *H. atratum* were spottily distributed, occurring mostly in three clusters of stations: 1) between lat 15° and 20°N in the *Washington* pattern, 2) between lat 10° to 15°S in the *Rockaway* pattern, and 3) an equatorial band between lat 5°N and 5°S along long 119°, 112°, and 105°W.

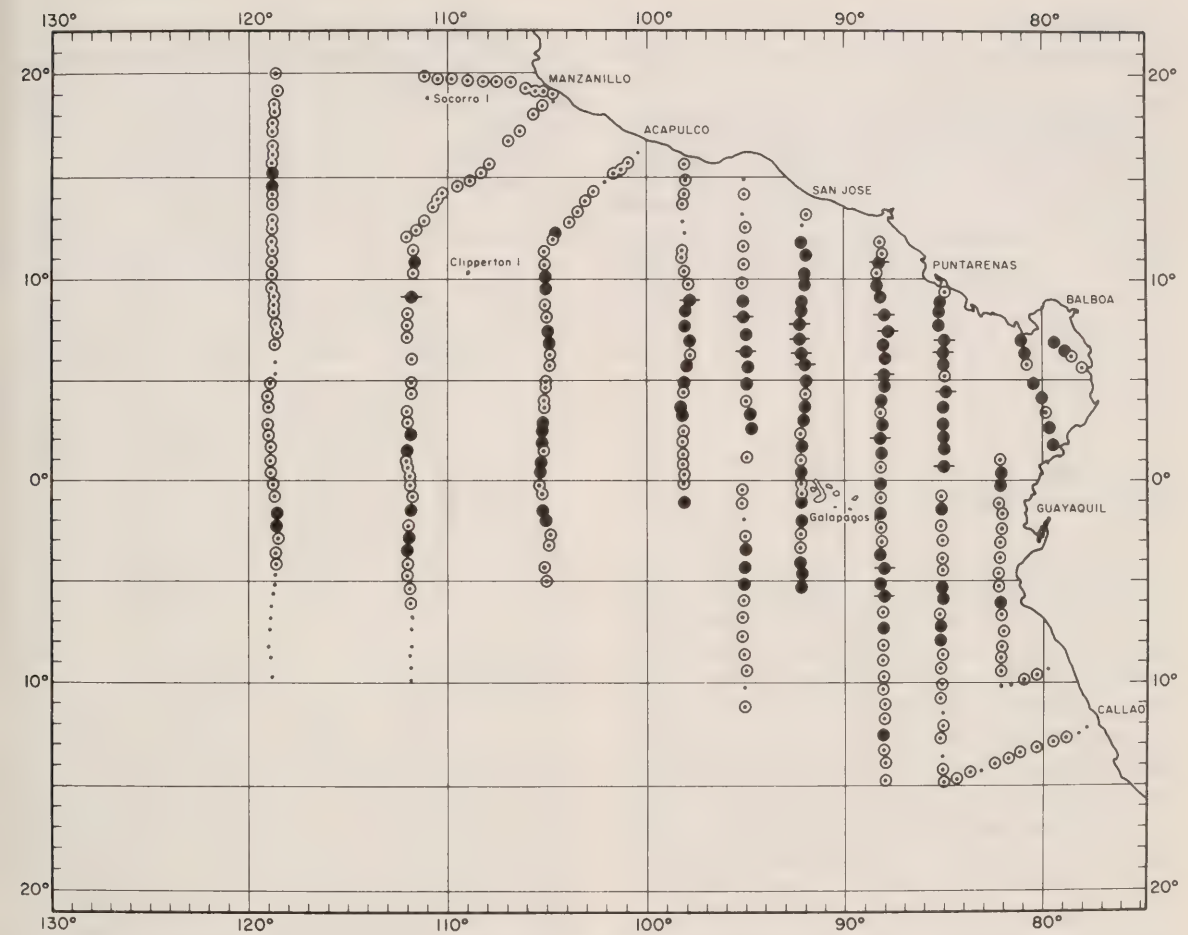

FIGURE 13.—Distribution of larvae of the myctophid *Diogenichthys laternatus* on ETP II. Three orders of abundance are shown. Open circles with dot represent counts of 1-100 larvae, large solid circles represent counts of 101-500 larvae, and large solid circles with bisecting line represent counts of 501 or more larvae; negative hauls are shown as small solid circles.

Hygophum proximum **(Becker)**
(77 occurrences, 624 larvae)

The distribution of larvae of *H. proximum* again is illustrated (Figure 8) to show the marked similarity in distribution to ETP I(Ahlstrom, 1971, Figure 10). Larvae of this species were decidedly more abundant in the offshore pattern occupied by *Washington* (55 occurrences, 499 larvae). As noted earlier, larvae of *H. proximum* were taken in somewhat greater abundance in ETP II as compared to equivalent ETP I (1.39×). Fully half of the occurrences and specimens of *H. proximum* larvae on ETP I was in the unreplicated portion of ETP I coverage, i.e., on the offshore line of stations along long 126°W and in the offshore southern portion of the pattern. There were three occurrences of larvae on ETP II in the southern part of the *Rockaway* pattern in transitional waters of the Humboldt Current; larvae were not obtained from this area on ETP I.

Lampadena sp.
(10 occurrences, 14 larvae)

Larvae of *Lamapadena* sp. were taken on the three offshore lines in two groups—one occurring between lat 3° and 8°N and the other in the central water mass of the South Pacific between lat 7° and 10°S. A similar distributional pattern was obtained on ETP I; however, the more extensive coverage of the South Pacific central water mass on the earlier survey provided better distributional information for the southern component.

Lampanyctus spp.
(291 occurrences, 5,334 larvae)

Lampanyctus larvae rank second in abundance and in frequency of occurrence among the myctophid genera represented in the eastern tropical Pacific. *Lampanyctus* larvae were most abundant between lat 5°N and 5°S and least common between lat 10° and 20°N. The six collections of *Lampanyctus* larvae that contained over 100 specimens per collection were taken between the equator and lat 5°N. Three kinds of *Lampanyctus* larvae dominated over most of the EASTROPAC pattern. Although identification to the species level are tentative as yet, these three kinds of larvae are almost certainly those of *L. idostigma* Parr, *L. omostigma Gilbert*, and *L. parvicauda* (Parr)—three widespread tropical species of *Lampanyctus*. A quite different assemblage of *Lampanyctus* larvae was taken in the moderate number of stations occupied in the South Pacific central water mass.

Lepidophanes pyrsobolus complex
(36 occurrences, 138 larvae)

An examination of the juvenile and adult specimens of *Lepidophanes* collected on ETP I has shown that two closely related species are present—one with a very restricted distribution and the other with a widespread distribution. Nafpaktitis and Nafpaktitis (1969) found three species of *Lepidophanes* from the Indian Ocean with common characteristics attributed to *L. pyrsobolus*. These workers considered Alcock's poorly described *L. pyrsobolus* as unidentifiable. Instead they identified their material with *L. photothorax* (Parr), *L. longipes* (Brauer), and *L. indicus* Nafpaktitis and Nafpaktitis. *L. photothorax* was taken in four ETP I collections between lat 15° and 20°S in the offshore pattern occupied by *Argo*. The specimens from the eastern Pacific agree closely with the description and illustration of this species in Nafpaktitis and Nafpaktitis (1969). These workers gave 7 + 4 as the usual combination of AO photophores on specimens from Indian Ocean material. In the EASTROPAC area all specimens examined had 6 + 4 AO photophores.

The widely distributed species in the EASTROPAC area is either *L. longipes* (Brauer) or a species closely related to *L. longipes*. The eastern Pacific form has similar luminous patches to those described for *L. longipes* from the Indian Ocean except for the luminous tissue on the head of males and the size of the infracaudal gland on some larger specimens. Luminous patches developed on the head were restricted to a single wide pair of luminous patches. On some larger specimens the infracaudal gland began under the last AO photophore and was conspicuously larger than those observed by Nafpaktitis and Nafpaktitis (1969) on Indian Ocean material. AO photophores were usually 5 + 4; gill raker counts were 5 + 1 + 11 to 13.

Two kinds of *Lepidophanes* have been observed in the EASTROPAC area, although only one kind was taken commonly. Larvae of the latter have been assigned to *L. longipes* (?).

Lobianchia spp.
(10 occurrences, 15 larvae)

Larvae of *Lobianchia*, although uncommon in the eastern tropical Pacific, have a fairly widespread distribution in two separated areas: 1) in an equatorial belt between lat 3°S and 6°N (8 occurrences) and 2) in the transitional waters of the Humboldt Current. In the latter area, two occurrences were recorded at about lat 12°

to 13°S along long 88°W, and three additional records were obtained at MARCHILE VI stations (not included in above totals). At least two species, *L. gemellari* (Cocco) and *L. dumerili* (Bleeker), and perhaps a third, are involved.

Loweina laurae (Wisner) (25 occurrences, 37 larvae)

Wisner (1971) has separated the eastern Pacific species of *Loweina* from *L. rara* (Lütken). Although the two species are basically quite similar, Wisner points out that *L. laurae* has a somewhat longer head, 27.3 to 30.7% of SL versus about 25.7%, and a somewhat larger eye, averaging about 8% of SL versus about 6%. Wisner gave the distribution of *L. laurae* in the eastern Pacific as between lat 30°N and 30°S and westerly to long 150°W.

Of the 25 occurrences of larvae of *L. laurae* on ETP II, all but one occurred in a broad equatorial band between lat 7°N and 6°S (Figure 14). The isolated record was on the southernmost line of stations oriented normal to the coast occupied by *Rockaway*. This distribution is similar to that illustrated for ETP I (Moser and Ahlstrom, 1970, Figure 51). In equivalent coverage on ETP I, 31 stations yielded 41 larvae. It should be noted that larvae of *Loweina* from EASTROPAC appear to be identical with those identified as *L. rara* from other oceans; hence larval evidence does not support the separation of the eastern Pacific form as a separate species.

Myctophum spp. (217 occurrences, 2,185 larvae)

Larvae of the genus *Myctophum* ranked fourth in abundance and third in frequency of occurrence. Larvae of *M. aurolaternatum* Garman (148 occurrences, 674 larvae) were taken more frequently but in lesser amounts than larvae of *M. nitidulum*-complex (134 occurrences, 1,291 larvae). Larvae of *M. aurolaternatum* were taken in all parts of the EASTROPAC pattern, but in largest numbers between the equator and lat 5°N. Most larvae of *M. nitidulum*-complex were taken in a broad equatorial band between lat 8°N and 5°S (Figure 11). The distribution, however, had a southerly extension to the bottom of the pattern in the area of the Humboldt Current. Larvae of *M. asperum* Richardson (26 occurrences, 180 larvae) were taken in an offshore equatorial tongue, extending seaward from long 98°W to its widest extent (lat 2°S to 7°N) along long 119°W (Figure 3). The remainder of *Myctophum* larvae (17 occurrences, 40 larvae) belong to two and possibly three species. One group of these occurred in the offshore equatorial tongue, along with larvae of *M. asperum;* the other group occurred between lat 7° and 10°S in the offshore *Washington* pattern. The latter group includes larvae of both *M. lychnobium* Bolin and *M. brachygnathos* (Bleeker).

Only larvae of *M. aurolaternatum* were separately tabulated for equivalent ETP I coverage (145 occurrences, 529 larvae). Both the distribution of *M. aurolaternatum* larvae and their frequency of occurrence were similar for the two multivessel surveys, although abundance was moderately greater on ETP II, 1.9 versus 1.5 larvae per haul. This pattern of greater abundance on ETP II also held for the remainder of the larvae of *Myctophum*, 4.3 versus 2.9 larvae per haul.

Notolychnus valdiviae (Brauer) (100 occurrences, 534 larvae)

Larvae of the wide-ranging oceanic species are seldom taken closer to shore than 200 miles. On ETP II, the majority of records were from an equatorial tongue that extended between lat 10°S and 10°N in the offshore *Washington* pattern, but shoreward of this (long 105° to 85°W) the distribution narrowed to between lat 2°S and 8°N, with the majority of occurrences between lat 2° and 6°N. A second group of larvae were sampled in the southern portion of the *Rockaway* pattern between lat 9° and 15°S. Only two occurrences of *Notolychnus* larvae were noted in 85 stations occupied by all vessels between lat 20° and 10°N. Distribution of *Notolychnus*

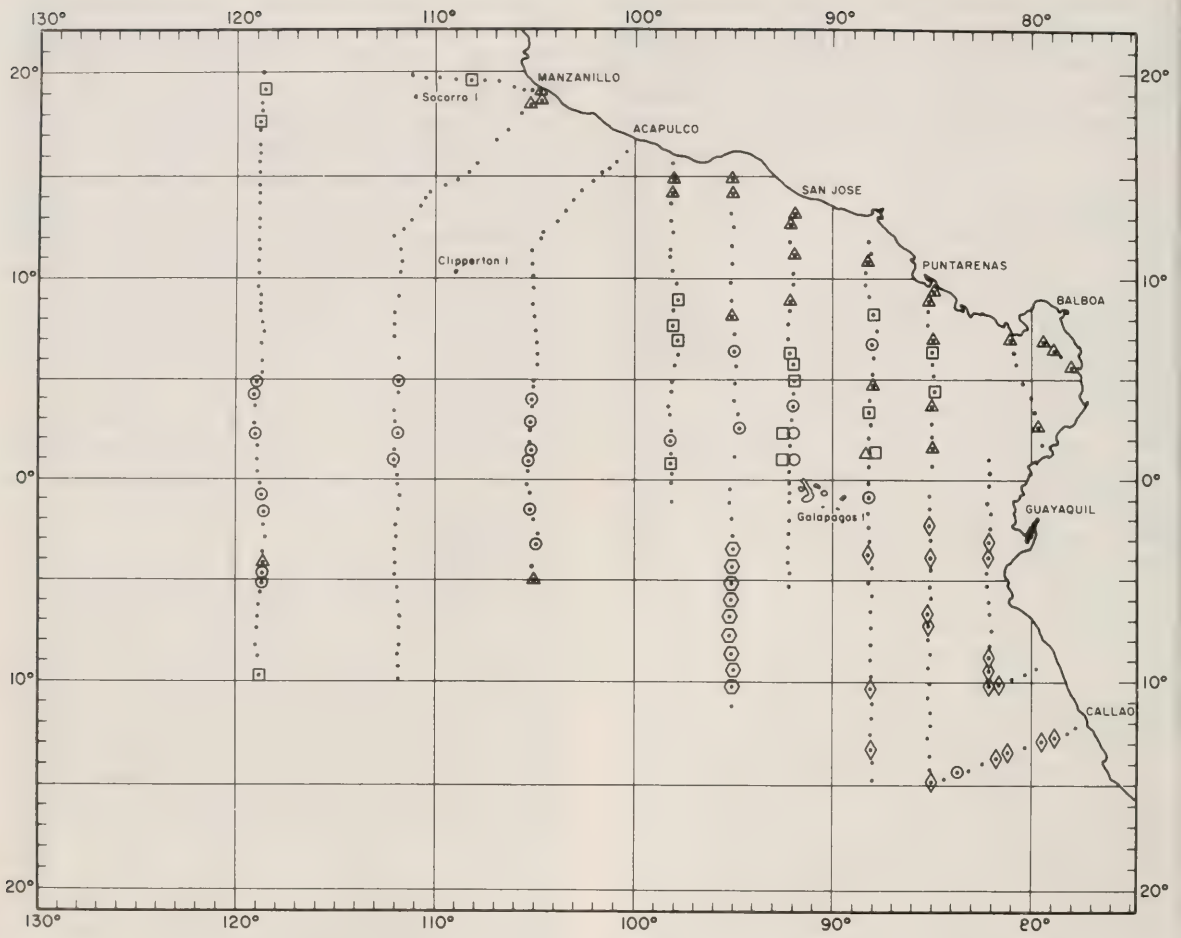

FIGURE 14.—Distribution of larvae of the myctophid, *Loweina laurae* (open circle with dot), of the scomberesocids, *Scomberesox saurus* (open diamond with dot), and *Cololabis adocetus* (open hexagon with dot) and of the anguilliform families Congridae (open triangle with dot) and Nemichthyidae (open square with dot); negative hauls are shown as small solid circles.

larvae was illustrated for ETP I coverage (Ahlstrom, 1971, Figure 11). In the portion of ETP I pattern also covered on ETP II, frequency of occurrence and distribution of *Notolychnus* larvae were quite similar: 1.7 versus 1.5 larvae.

Notoscopelus resplendens (Richardson)
(78 occurrences, 382 larvae)

As on ETP I, most larvae of *N. resplendens* were taken in an equatorial belt, between lat 5°N and 5°S (65 occurrences, 364 larvae). A second center of occurrence was at the southern portion of the *Rockaway* pattern between lat 9° and 15°S. Except that the distribution of the main group of *Notoscopelus* larvae is more definitely centered on the equator, the distribution of larvae of *Notoscopelus* and *Notolychnus* are quite similar. No larvae of *Notoscopelus* were taken north of lat 6°N. Moderately more larvae of *Notoscopelus* were taken on ETP II, 1.1 versus 0.7 larvae per haul.

Protomyctophum sp.
(25 occurrences, 44 larvae)

For most kinds of myctophids, the distributional patterns of larvae are so similar in the two multivessel EASTROPAC survey cruises that distributional information from ETP II merely reinforced that obtained on ETP I. Distribution of *Protomyctophum* larvae affords another example of this. All but two of the occurrences lie between lat 10°N and 5°S, the zone in which all *Protomyctophum* larvae were obtained on ETP I. As noted in Ahlstrom (1971), the larvae were all of a kind, belonging to a perhaps undescribed species of *Protomyctophum*, subgenus *Hierops*. Wisner (1971) described two new species of *Protomyctophum*, subgenus *Hierops* from the eastern Pacific: *P. chilensis* from off Chile about lat 33°S and *P. beckeri* from the vicinity of the Hawaiian Islands. It is not known as yet whether the form from EASTROPAC is referable to either of these.

Symbolophorus evermanni (Gilbert)
(155 occurrences, 822 larvae)

Larvae of *Symbolophorus* were absent from a wide coastal strip off Mexico and a narrower coastal strip off Peru, but were taken at most stations in the remainder of the ETP II pattern. The distribution was rather similar to that illustrated for ETP I (Ahlstrom, 1971, Figure 12); the frequency of occurrence was slightly lower on equivalent ETP I (37% positive hauls versus 44%), but the average abundance per haul was slightly higher (2.6 versus 2.3 larvae). However, in the ETP I stations without counterparts in ETP II, frequency of occurrence was higher than in the remainder of the ETP I pattern (63% versus 37%) and average abundance per haul was higher (4.5 versus 2.6 larvae).

Triphoturus spp.
(144 occurrences, 824 larvae)

Larvae of *Triphoturus oculeus* (Garman) were taken in most hauls made between lat 5°N and 15°S off Ecuador and Peru and offshore to the vicinity of the Galapagos Islands. Larvae of this species, which appear to be more exclusively restricted to the transition waters of the Humboldt Current than are those of other myctophids sampled in the EASTROPAC pattern, also may exhibit the most marked seasonal change in relative abundance. Other *Triphoturus* larvae, sampled mostly offshore, were taken in slightly lesser abundance than on ETP I.

16. PARALEPIDIDAE
(247 occurrences, 2,535 larvae)

Larvae of Paralepididae ranked sixth in abundance and contributed over 2% of the total. Larvae were taken throughout the ETP II pattern, but most commonly in an equatorial band between lat 5°N and 5°S; all collections of larvae exceeding 25 larvae per haul were obtained from this band. Fewest larvae were taken in the southern portion of the inner pattern, below about lat 7°S. Because of limited coverage of the South Pacific central water mass on ETP II, no material was obtained of *Sudix atrox* Rofen (see Ahlstrom, 1971, Figure 7 for distribution of larvae of this species on ETP I). A detailed study of the species composition of the paralepidid material from EASTROPAC surveys has not been made.

17. SCOPELARCHIDAE
(134 occurrences, 298 larvae)

Larvae of Scopelarchidae were taken throughout the area surveyed on ETP II. As noted for ETP I (Ahlstrom, 1971, p. 32-33), larvae of five or six kinds of scopelarchids were obtained, usually in small numbers per haul. On ETP II, only 6 of 133 positive hauls contained over 5 larvae (6 to 12 larvae), and over 80% of the hauls contained 1 to 3 larvae per haul.

18. SCOPELOSAURIDAE
(40 occurrences, 390 larvae)

Larvae of Scopelosauridae were taken in more

hauls and in much larger numbers than on equivalent ETP I (6 occurrences, 13 larvae). As shown in Figure 10, most occurrences were in an equatorial band between lat 5°N and 5°S and offshore to long 105°W; the five hauls containing 25 or more larvae were obtained within 2° of the equator. Only one kind of *Scopelosaurus* larva was obtained on ETP II. Larvae of *Scopelosaurus* superficially resemble paralepidid larvae—both have elongate larvae with a short gut that increases in relative length in older larvae. However, *Scopelosaurus* larvae differ in several significant ways from paralepidid larvae. *Scopelosaurus* larvae never develop patches of pigment above the intestinal tract, whereas these patches are a striking feature of paralepidid larvae; the eyes of *Scopelosaurus* larvae are narrowed, whereas they are round in most paralepidid larvae; also the intestinal tract does not increase in relative length nearly as much in older stage *Scopelosaurus* larvae as in paralepidid larvae.

19. SYNODONTIDAE
(14 occurrences, 60 larvae)

Larvae of *Synodus* spp. occurred in a coastal band along the extent of the ETP II pattern (Figure 5). Six species of *Synodus* are known to occur in the eastern Pacific. Several kinds of *Synodus* larvae were taken in the EASTROPAC collections, mostly small specimens. Until more older-stage larvae are obtained, it will not be possible to work out life history series.

21. ANGUILLIFORMES (EEL LEPTOCEPHALI)
(81 occurrences, 151 larvae)

Eel leptocephali, although conspicuous members of the larval fish fauna, are not common in the EASTROPAC pattern: they contributed only 0.12% of the total ETP II larvae. Leptocephali of seven families of true eels of the order Anguilliformes, suborder Anguilloidei, were identified from the micronekton net collections of ETP II. The micronekton net collections from ETP I contributed three times as many leptocephali as the regular net hauls; a total of 10 families was represented in the combined ETP I collections, including the 7 discussed below and in addition Derichthyidae, Muraenesocidae, and Nettastomidae. The record of occurrence and counts by family of eel leptocephali on all positive stations is contained in Appendix Table 5, and summarized in Table 20. The distributions of larvae of the seven families taken in ETP II collections are shown in Figures 14 and 15.

Congridae
(28 occurrences, 42 larvae)

This family ranked first in frequency of occurrence among eel leptocephali and second in relative abundance. Most congrid larvae were identifiable to genus. The breakdown was as follows: *Ariosoma* sp. (5 occurrences, 8 larvae), *Bathyconger* sp. (3 occurrences, 4 larvae), *Gnathopis* sp. (1 occurrence, 1 larva), *Hildebrandia* (10 occurrences, 18 larvae), *Paraconger* (4 occurrences, 5 larvae), and genus uncertain (6 occurrences, 6 larvae). All but two occurrences were from north of the equator, and most specimens were taken in a broad coastal band. However, offshore oceanic occurrences of congrid leptocephali were more frequent on ETP I than on ETP II.

Moringuidae
(3 occurrences, 3 larvae)

One occurrence of leptocephali of the moringuid genus *Neoconger* was off Manzanillo, Mexico, the other two near Panama Bay.

Muraenidae
(5 occurrences, 6 larvae)

Although adults of Muraenidae are known to have a wide distribution in the eastern Pacific, the few leptocephali taken on ETP II were confined to a narrow tongue extending offshore between lat 7° and 10°N in the northeast quadrant.

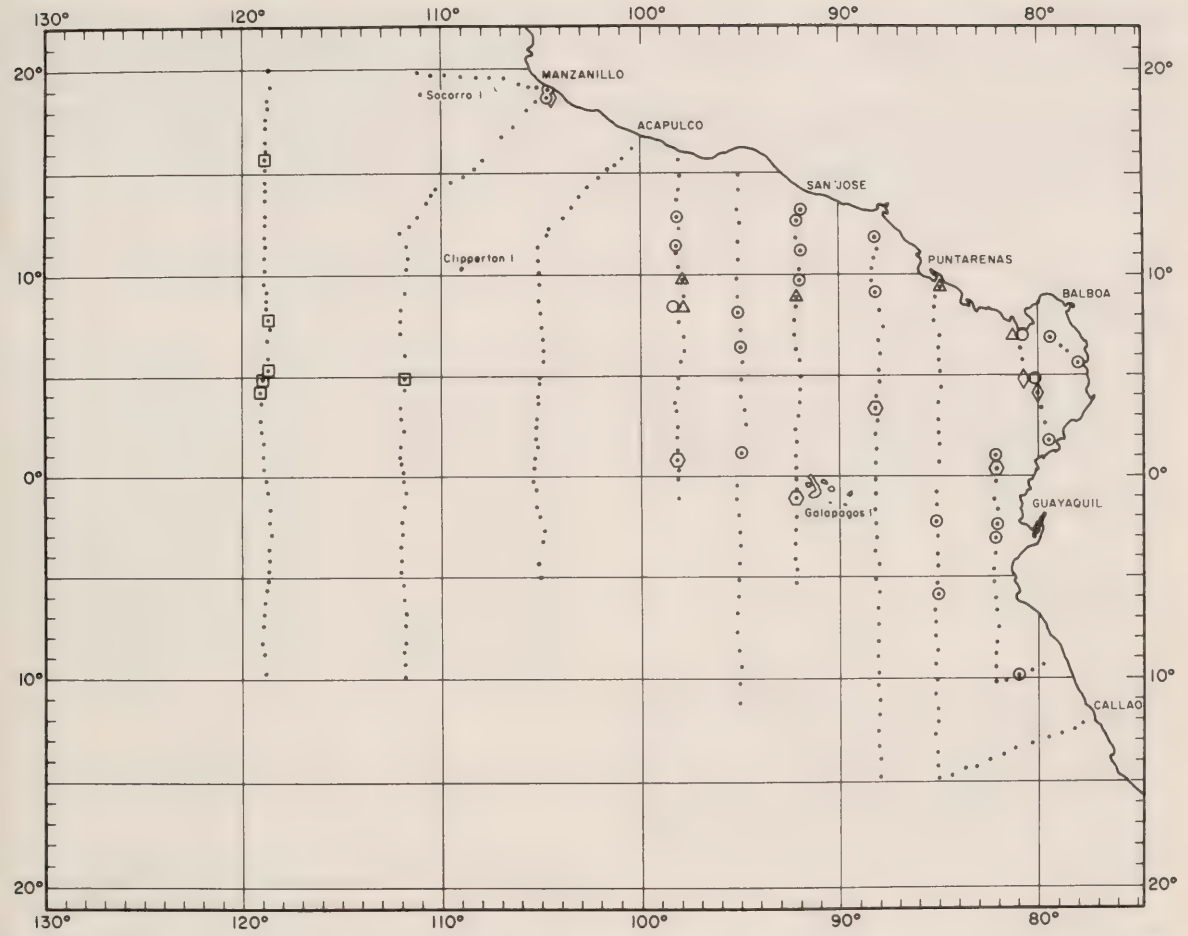

FIGURE 15.—Distribution of eel leptocephali of the anguilliform families: Moringuidae (open diamond with dot), Muraenidae (open triangle with dot), Opichthidae (open circle with dot), Serrivomeridae (open square with dot), and Xenocongridae (open hexagon with dot); negative hauls are shown as small solid circles.

TABLE 20.—Familial composition of eel leptocephali taken on the second multivessel EASTROPAC survey, summarized by vessel pattern.

Family	*Washington* 45.000 series		*Undaunted* 46.000 series		*Rockaway* 47.000 series		Total EASTROPAC II	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
Congridae	3	6	9	11	16	25	28	42
Moringuidae	1	1	0	0	2	2	3	3
Muraenidae	0	0	3	3	2	3	5	6
Nemichthyidae	4	5	9	9	6	7	19	21
Ophichthidae	2	8	7	12	17	29	26	49
Serrivomeridae	6	8	0	0	0	0	6	8
Xenocongridae	0	0	2	2	2	2	4	4
Family unknown	4	5	4	5	5	8	13	18
Total	16	33	30	42	35	76	81	151

Nemichthyidae
(19 occurrences, 21 larvae)

Although eels of this family are widely distributed in offshore oceanic waters, most occurrences of leptocephali (14 of 19) were in the northeast quadrant, between lat 0° and 10°N.

Ophichthidae
(26 occurrences, 49 larvae)

Ophichthid leptocephali were taken in a broad coastal band between Manzanillo, Mexico, and Central Peru (lat 10°S). They ranked first in relative abundance among eel leptocephali and second in frequency of occurrence.

Serrivomeridae
(6 occurrences, 8 larvae)

Most occurrences of serrivomerid leptocephali (5 of 6) were on the outer line of the ETP II pattern, along long 119°W, and the remaining occurrence was along long 112°W. In contrast to nemichthyid leptocephali which may grow to 300 or 400 mm long, leptocephali of Serrivomeridae rarely exceed about 60 mm.

Xenocongridae
(4 occurrences, 4 larvae)

The few occurrences of leptocephali of *Chlopsis*, the sole representative of this family, were within 4° of the equator.

22. MELAMPHAIDAE
(284 occurrences, 1,365 larvae)

Larvae of Melamphaidae ranked fourth in frequency of occurrence, eighth in relative abundance. Larvae were distributed throughout the ETP II pattern (Figure 16) and occurred in 80% of the collections. Most collections contained only moderate numbers of larvae—the average number of larvae per positive haul was only 4 to 8. The majority of hauls containing larger numbers of larvae (11 or more per haul) were taken within 5° of the equator (Figure 16). Melamphaid larvae were represented by four genera: *Melamphaes*, *Scopelogadus*, *Scopeloberyx*, and *Poromitra*.

23. TRACHICHTHYIDAE
(11 occurrences, 70 larvae)

The big-headed larvae of a representative of this family were taken at 11 stations on the two inner lines of the *Rockaway* pattern, between about lat 2° to 8°S (Appendix Table 3). They appear to be larvae of *Trachichthys mento* Garman, initially described from the Gulf of Panama. Bussing (1965) supplemented Garman's description, utilizing 53 specimens (55 to 104 mm) collected at *Eltanin* Station 34 at lat 07°45′ to 07°48′S, long 81°23′W. Parin (1971) also obtained material of this species in the eastern tropical Pacific from off South America.

25. BREGMACEROTIDAE
(160 occurrences, 3,062 larvae)

Larvae of Bregmacerotidae ranked fifth in abundance and contributed 2.5% of fish larvae on ETP II. The majority of larvae was taken to the north of the equator, with three inshore collections contributing over 70% of the total. These collections of 927, 753, and 511 larvae were exclusively *Bregmaceros bathymaster* Jordan. Larvae of this species were distributed in a broad coastal band in the northern half of the EASTROPAC pattern. As noted in the ETP I report, larvae of five species of *Bregmaceros* are distributed in the eastern tropical Pacific.

27. SCOMBERESOCIDAE
(27 occurrences, 153 specimens)

Two species of Scomberescocidae were taken on ETP II—*Scomberesox saurus* L. (18 occurrences, 52 specimens) and *Cololabis adocetus* Böhlke (9 occurrences, 101 specimens). The

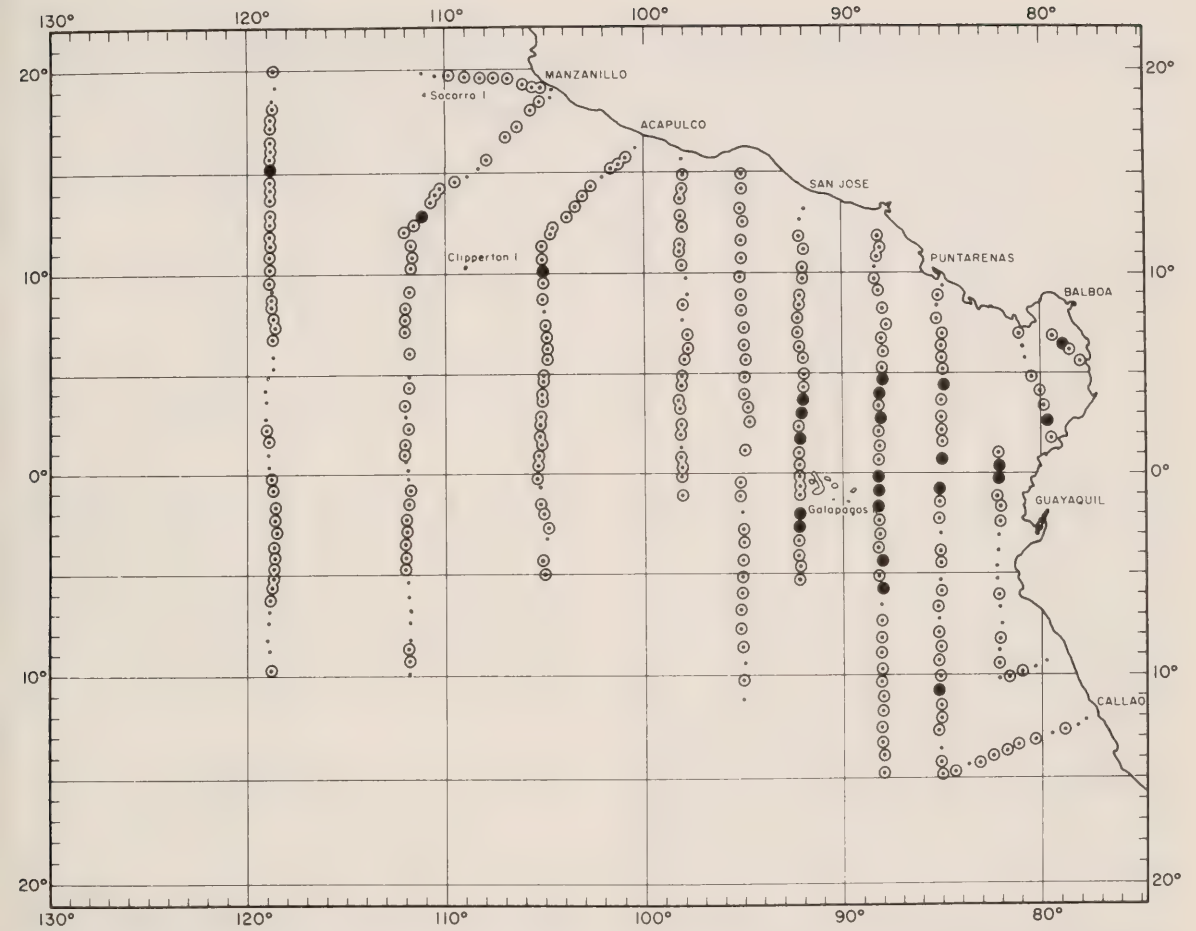

FIGURE 16.—Distribution of larvae of the beryciform family Melamphaidae on ETP II. Collections of 1-10 larvae are shown as open circles with dot, collections of 11 or more larvae as large solid circles; negative hauls are shown as small solid circles.

word "specimen" is used intentionally because some juveniles as well as larvae are included in the above counts. A number of the specimens were x-rayed in order to obtain vertebral counts to verify identification. All occurrences of the small tropical saury, *Cololabis adocetus*, were along long 95°W at nine contiguous stations (Figure 14); surface temperatures ranged between 19.5° and 21.5°C at these stations. *Scomberesox* larvae occurred in a broad coastal belt, shoreward of *C. adocetus*, extending from near the equator to the southernmost line occupied on ETP II (Figure 14); surface temperatures ranged between 15.8° and 19.5°C at these stations. Actually *Scomberesox* eggs and larvae were commonly taken in the pattern occupied by *Yelcho* off Chile as part of ETP II—MARCHILE VI. Collections obtained from surface tows as well as from oblique net hauls were available from MARCHILE VI. Five short lines of stations normal to the trend of the Chilean coastline were occupied on MARCHILE VI, between lat 18°30′ and 33°S. *Scomberesox* eggs and larvae were sampled best in surface hauls. *Scomberesox* eggs were taken in 17 of 20 surface hauls and *Scomberesox* larvae in 10 surface

TABLE 21.—Measurements of eggs of *Scomberesox saurus* collected on EASTROPAC II, including collections made off Chile by *Yelcho* (MARCHILE VI).

Collection	Type of haul	Locality of collection		Number eggs measured	Range in egg diameter (*mm*)	Average diameter (*mm*)	Surface water temperature (°C)
		Lat S	Long W				
MAR. 5.4	Surface	33°05.3′	73°20.5′	25	2.41-2.67	2.52	12.50
MAR. 4.4	Oblique	28°30.6′	72°43.2′	23	2.39-2.65	2.52	12.09
ETP 47.177	Oblique	06°35.0′	85°08.5′	31	2.31-2.60	2.44	18.14
MAR. 4.1	Surface	28°30.2′	71°40.1′	30	2.26-2.62	2.43	11.93
MAR. 3.2	Surface	23°42.5′	71°35.0′	25	2.24-2.45	2.36	14.39
ETP 47.145	Oblique	14°17.8′	83°03.7′	14	2.26-2.43	2.35	18.28
MAR. 1.8	Surface	18°27.6′	73°06.1′	25	2.24-2.51	2.34	15.81 (10 *m*)
ETP 47.134	Oblique	12°56.5′	79°27.8′	16	2.21-2.48	2.34	16.62
ETP 47.103	Oblique	10°09.0′	82°08.5′	25	2.26-2.45	2.34	18.32
ETP 47.107	Oblique	09°50.0′	80°53.0′	16	2.26-2.46	2.34	17.74
MAR. 2.1	Surface	20°09.0′	70°31.8′	25	2.15-2.45	2.33	15.77 (10 *m*)
MAR. 1.4	Surface	18°32.0′	71°42.0′	25	2.17-2.45	2.32	15.92 (10 *m*)
MAR. 2.4	Surface	20°10.8′	71°33.2′	25	2.19-2.45	2.32	15.74 (10 *m*)

hauls on MARCHILE VI. Hence young of *Scomberesox* have a north-south extent off South America of at least 1,860 miles.

Scomberesox eggs are approximately round and occur singly—lacking the attachment filaments characteristic of most eggs of fishes in the suborder Exocoetoidei (see in this regard Orton, 1964). The egg shell, however, is ornamented with minute closely spaced swellings. Eggs from 13 collections were measured (eggs measured in widest dimensions as they were not truly spherical); the data are summarized in Table 21. The range in egg size was from 2.15 to 2.67 mm; the range in egg diameter means for the 13 collections was from 2.32 to 2.52 mm. Eggs in the majority of collections (9 of 13) were quite similar in average diameters, ranging between 2.32 and 2.36 mm. Three of the four collections of eggs with larger average diameters were taken on the southernmost two lines of the *Yelcho* pattern. However, the collection of eggs made nearest to the equator (lat 6°35′) also was in this group of larger eggs.

30. APOGONIDAE

(66 occurrences, 283 larvae)

This family contains both oceanic and coastal species. Larvae of coastal apogonids were taken in four hauls off Central America and northern South America. The remainder of the larvae (62 occurrences, 278 larvae) were those of *Howella pammelas* (Heller and Snodgrass). Larvae of this species were most common to the north of the equator in a broad band extending offshore between 0° and lat 9°N. Only three occurrences were found to the north of this band and 11 to the south. This species was not limited in its distribution to particular water masses.

34. CARANGIDAE

(36 occurrences, 224 larvae)

Larvae of the pilotfish, *Naucrates ductor* (L.), with 18 occurrences, 27 larvae (Figure 17), was the most widely distributed carangid on ETP II. Over half of the carangid larvae were obtained at two coastal stations—45 larvae at 46.135 and 69 larvae at 47.527. As on ETP I, a number of kinds of carangid larvae were taken, including *Chloroscombrus orqueta* Jordan and Gilbert, *Selene brevoorti* (Gill), and *Caranx* spp.

37. CORYPHAENIDAE

(109 occurrences, 185 larvae)

Larvae of the dolphin, *Coryphaena* spp., were taken almost exclusively to the north of the equator (105 occurrences, 180 larvae) on ETP II; three of the four occurrences to the south of the equator were at stations immediately adjacent to the equator. *Coryphaena* larvae were

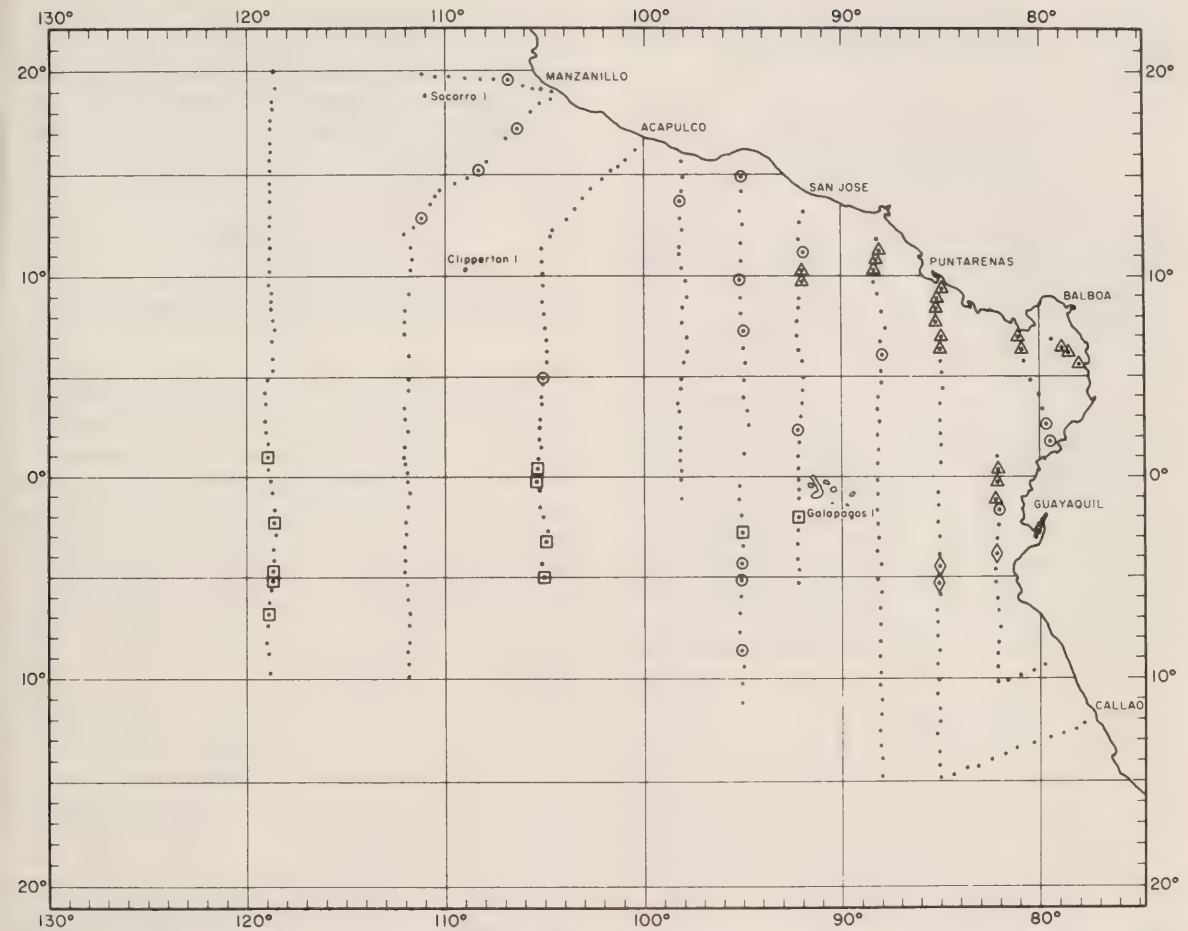

FIGURE 17.—Distribution of larvae of the carangid, *Naucrates ductor* (open circle with dot), of the tetragonurid, *Tetragonurus* spp. (open square with dot), and of the trichiurids, *Lepidopus* sp. (open diamond with dot) and *Trichiurus lepturus* (open triangle with dot); negative hauls are shown as small solid circles.

taken throughout the coverage on ETP I but at a lesser proportion of the stations; in equivalent coverage, 97 larvae were taken in 67 collections on ETP I. Dolphin larvae provide one of the more striking examples of a marked difference in the distributional pattern of larvae as between ETP I and ETP II.

Eggs and newly hatched larvae have been described for *Coryphaena hippurus* L. by Mito (1960). The eggs are 1.2 to 1.6 mm, with a single oil globule 0.3 to 0.4 mm. The larvae are heavily pigmented, even at hatching. We have not found distinguishing characters to separate the larvae of *C. hippurus* from those of *C. equiselis,* hence have labelled our material as *Coryphaena* spp. After the vertebral column is developed, definitive identification can be made: *C. hippurus* has 31 vertebrae, *C. equiselis* has 33 (Collette, Gibbs, and Clipper, 1969). Parin (1968) reports that *C. hippurus* reproduces only in the littoral zone and that *C. equiselis* is the offshore spawner. If this pattern of spawning holds for the eastern Pacific, then the majority of larvae taken on EASTROPAC cruises were those of *C. equiselis.* As noted for this family in the first EASTROPAC paper (ETP I, 38) the

majority of the specimens obtained were early stage larvae, hence spawned in the area of collection.

38. GEMPYLIDAE

(112 occurrences, 370 larvae)

Two kinds of gempylid larvae were widely distributed in the EASTROPAC area on ETP II: larvae of *Gempylus serpens* Cuvier and Valenciennes (71 occurrences, 152 larvae) and *Nealotus tripes* Johnson (66 occurrences, 218 larvae).

Larvae of both species had a higher frequency of occurrence and greater abundance on ETP II. Distribution within the EASTROPAC area also was different in the two multivessel surveys. The more widespread distributional pattern for *Gempylus serpens* was observed from the wider-ranging ETP I survey. Over a third of the occurrences of *Gempylus* larvae were in the portion of the ETP I pattern not replicated on ETP II (Ahlstrom, 1971, Figure 13). Larvae were taken throughout the ETP I pattern with as many records from south of the equator as to the north. In contrast, only three collections were made to the south of the equator on ETP II (Figure 4), but many more collections of *Gempylus* larvae were obtained to the north of the equator, particularly in the inner pattern occupied by *Rockaway*.

Changes in distribution of larvae of *Nealotus tripes* in the two surveys were not as marked as for *G. serpens*. On both surveys the majority of the occurrences of *Nealotus* larvae were in the inner half of the ETP pattern; heaviest concentration of larvae on ETP II was in an equatorial band between circa lat 5°N and 3°S. Fewer *Nealotus* larvae were taken in the inner pattern off Peru, between circa lat 3° and 15°S, as compared with ETP I (ETP I, Figure 7).

39. GOBIIDAE

(53 occurrences, 384 larvae)

Larvae of several families of shore or bottom fishes have a much more widespread oceanic distribution than would be anticipated from the distribution of adults. In the EASTROPAC area this applies particularly to larvae of Gobiidae, Scorpaenidae, Labridae, Bothidae, and Cynoglossidae. Based on pigmentation and meristics a minimum of eight kinds of goby larvae were taken.

42. NOMEIDAE

(229 occurrences, 1,460 larvae)
And other Stromateiodei (14 occurrences, 16 larvae)

Four families of stromateoid, fishes were taken on EASTROPAC cruises: Amarsipidae, Nomeidae, Stromateidae, and Tetragonuridae. Three of these families contain oceanic species that are widely distributed in offshore waters; only fishes of the family Stromateidae are confined to coastal waters. Important papers dealing with stromateoid fishes include Grey (1955), Haedrich (1967, 1969), Haedrich and Horn (1969),[2] and Horn (1970).

In the EASTROPAC area, only the nomeids were common, occurring in about two-thirds of the collections made on ETP II. Larvae were obtained of two genera, *Cubiceps* and *Psenes;* larvae of the former were the more abundant, larvae of the latter were more diversified as to species represented.

Larvae of a species in the family Stromateidae, *Peprilus medius* (Peters), were taken at a single station on ETP II, 46.135 (2 larvae), but a larger collection was obtained at *Oceanographer* Station OP 168 (16 larvae).

Larvae of Tetragonuridae (11 occurrences, 12 larvae) occurred in an equatorial band between lat 2°N and 7°S, seaward of the Galapagos Islands (Figure 17). As noted in the first EASTROPAC report, larvae of two species were taken: *T. cuvieri* Risso and *T. atlanticus* Lowe.

Two specimens of *Amarsipus carlsbergi,* described by Haedrich (1969) as a monotypic representative of a new family Amarsipidae, were

[2] Haedrich, R. L., and M. H. Horn. 1969. A key to the stromateoid fishes. Woods Hole Oceanogr. Inst. Ref. #69-70, 46 p. (Unpublished manuscr.)

obtained on ETP II, and five specimens previously had been taken on ETP I. These had been identified as *Centrolophus*-like with the notation that they probably represented an undescribed form. Identification of the material as *Amarsipus carlsbergi* was made by Dr. Michael H. Horn. Since little is known about this species in the eastern Pacific, I am listing all catch localities.

ETP II = Station 45.346 at lat 14°38.2′N, long 109°37.1′W, Sept. 8, 1967, 1 specimen, 26.2 mm; Station 47.272 at lat 11°20.8′N, long 88°00.5′W, Aug. 31, 1967, 1 specimen, 15.0 mm.

ETP I = Station 11.066 at lat 06°49.8′N, long 118°55.5′W, Feb. 3, 1967, 1 specimen, 10.3 mm; Station 11.114 at lat 02°37.8′S, long 119°02.3′W, Feb. 7, 1967, 1 specimen, 30.0 mm; Station 11.306 at lat 12°03.5′N, long 126°00′W, Feb. 27, 1967, 1 specimen, 16.0 mm; Station 12.059 at lat 09°31.5′N, long 105°02.0′W, Feb. 22, 1967, 1 specimen, 7.2 mm; Station 12.246 at lat 06°12.0′N, long 112°00.5′W, Mar. 16, 1967, 1 specimen, 7.3 mm.

43. OPHIDIIDAE

(38 occurrences, 81 larvae)

A number of kinds of larvae of this complex family were taken on ETP II, mostly in a coastal band between Acapulco, Mexico, and central Peru, but six occurrences were in a loose cluster about the Galapagos Islands. Only one kind has been identified to genus as yet; this is a form with conspicuously large pectorals (11 occurrences, 15 larvae) whose larvae were clustered in the Gulf of Panama or immediately seaward. Dr. Daniel Cohen of the National Marine Fisheries Service has identified larger specimens (small juveniles) as *Brotula* sp. A characteristic of this genus observed on several specimens was the presence of two ural centra in the "urostyle." Garman (1899) described 22 species of ophidiid-brotulids from the eastern tropical Pacific, few of which have been retaken subsequently. However, the variety of kinds of ophidiid larvae in our material attests to a speciose fauna.

47. SCOMBRIDAE

(55 occurrences, 248 larvae)

Scombrid larvae were markedly less abundant in ETP II as compared with similar coverage on ETP I (163 occurrences, 1,840 larvae).

The majority of scombrid larvae from ETP II were those of *Auxis* sp. (34 occurrences, 151 larvae) or were too small to identify with certainty (30 occurrences, 84 larvae). The remaining scombrid larvae included the wahoo, *Acanthocybium solanderi* (Cuvier) (2 occurrences, 3 larvae) from Stations 45.065 and 46.004; the mackerel, *Scomber japonicus* Hottuyn, (2 occurrences, 4 larvae) from near the Galapagos Islands; bigeye tuna, *Thunnus obesus* Lowe, (1 occurrence, 1 larva); skipjack, *Katsuwonus pelamis* (Linnaeus), (2 occurrences, 2 larvae); yellowfin tuna, *Thunnus albacares* (Bonnaterre), (2 occurrences, 2 larvae). Scombrid larvae were given to W. Klawe of the Inter-American Tropical Tuna Commission for identification.

52. TRICHIURIDAE

(49 occurrences, 186 larvae)

In the ETP I contribution, I pointed out the similarity in appearance of larvae of *Diplospinus multistriatus* Maul and those of *Gempylus serpens,* and the problems this raised about the distribution of genera between Gempylidae and Trichiuridae and perhaps about the need for two families. Treating larvae of the two families separately in this paper was done only for convenience. The problems raised in the first ETP contribution still need to be solved.

Three kinds of trichiurid larvae were obtained on ETP II: larvae of *D. multistriatus* Maul, *Trichiurus lepturus* (L.), and *Lepidopus* sp.

The distribution of larvae of *D. multistriatus* (25 occurrences, 69 larvae) was strikingly similar on the two multivessel cruises (Figure 4 and Ahlstrom, 1971, Figure 14). On ETP II, all but two occurrences were in a compact group at the southern inner half of the ETP pattern between circa lat 8° and 15°S and offshore to long 95°W. Most ETP I collections of larvae of this species were obtained from this same

general area. The remaining two occurrences on ETP II were obtained at the northern, outer end of the pattern, again similar to the distribution of *Diplospinus* larvae on ETP I. On ETP II, there were no occurrences of *Diplospinus* larvae between these two widely separated groups; on ETP I two specimens were taken at intermediate localities. Larvae of this species have been obtained in a number of collections made in the North Pacific central water mass, with best distributional information from the NORPAC Expedition of August 1955. It is not taken in California Current waters, hence the distribution in the Humboldt Current waters off Peru does not have a mirror-image replication in the California Current, as has been found for a number of species.

Larvae of *Trichiurus lepturus* (20 occurrences, 106 larvae) were taken in a coastal band on ETP II (Figure 17). Eggs of this species are readily identified and occurred in many of the hauls containing *Trichiurus* larvae and in some additional hauls. Interestingly enough, larvae of this species were not obtained in ETP I collections, hence this is another exception to the general pattern of year-long reproduction by tropical pelagic fishes. Unlike larvae of *Gempylus* or *Nealotus*, which were widely distributed in the EASTROPAC area, larvae of this species appear to have a restricted, coastal distribution.

Larvae of *Lepidopus* sp. (3 occurrences, 9 larvae) were taken in contiguous stations at about lat 5°S off Peru (Figure 17). Larvae of *Lepidopus* were taken in more hauls on ETP I (7 occurrences, 25 larvae, Ahlstrom, 1971, Figure 14), all located between the equator and lat 5°N and offshore to long 92°W.

This change in area of spawning of *Lepidopus* from north of the equator on ETP I to the south of the equator on ETP II may not be significant, because of the paucity of positive hauls. If real, one can only surmise as to whether the two populations were discrete, with separate spawning seasons on the two sides of the equator.

53. BOTHIDAE

(70 occurrences, 690 larvae)

Bothid larvae occurred in more hauls than on ETP I (70 versus 56 occurrences) and in larger numbers (690 versus 199 larvae). The species composition, however, was similar (Table 22). A short section will be devoted to each of the forms listed in this table.

Bothus leopardinus (Günther)

(27 occurrences, 97 larvae)

Only larvae of *B. leopardinus* have been ob-

TABLE 22.—Frequency of occurrence and relative abundance of larvae of flatfishes, Pleuronectiformes, on the second multivessel EASTROPAC survey, summarized by vessel pattern.

Flatfish larvae	*Washington* 45.000 series		*Undaunted* 46.000 series		*Rockaway* 47.000 series		Total EASTROPAC II	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
BOTHIDAE								
Bothus leopardinus	2	2	15	45	10	50	27	97
Citharichthys-Etropus	1	1	5	35	11	34	17	70
Cyclopsetta sp.	0	0	4	26	9	12	13	38
Engyophrys sancti-laurentii	0	0	0	0	3	3	3	3
Monolene sp.	0	0	0	0	1	1	1	1
Syacium ovale	6	15	17	201	32	264	55	480
Other Bothidae	1	1	0	0	0	0	1	1
Total Bothidae	7	19	28	307	35	364	70	690
CYNOGLOSSIDAE								
Symphurus spp.	2	5	16	109	38	248	56	362
Total Pleuronectiformes	7	24	30	416	46	612	83	1,052

tained in EASTROPAC collections. Although *B. mancus* (Broussonet) has been recorded from Clarion Island, off the west coast of Mexico (Norman, 1934), larvae of this species have not been obtained. Larval material of *B. mancus* has been examined from the vicinity of the Hawaiian Islands, and it differs from *B. leopardinus* in developing pigment on late stage larvae.

Larvae of *B. leopardinus* were distributed in a broad coastal band between Manzanillo, Mexico, and lat 4°N (Figure 8). This distribution is more restricted than that found on ETP I (Ahlstrom, 1971, Fig. 10). On ETP I, there were nine occurrences between lat 5°N and 6°S, as compared with a single occurrence on ETP II.

Citharichthys-Etropus
(17 occurrences, 70 larvae)

Although labeled *Citharichthys-Etropus* as for ETP I, the larvae taken on ETP II probably represent two species of *Citharichthys*, one with three elongated dorsal rays, the other with two elongated rays. Larvae of the latter were taken below the equator, either off Ecuador or near the Galapagos Islands (9 occurrences, 48 larvae). The form with three elongated dorsal rays was distributed in a coastal band between Manzanillo, Mexico, and Ecuador (8 occurrences, 22 larvae).

***Cyclopsetta* sp.**
(13 occurrences, 38 larvae)

Larvae of *Cyclopsetta* sp. occurred in a broad coastal band between lat 15°N and circa lat 5°S. The larvae have been identified tentatively as *C. querna* (Jordan and Bollman). A developmental series was recently described by Gutherz (1970) for an Atlantic species of this genus, *C. fimbriata* (Goode and Bean). The Pacific and Atlantic species are similar in having opercular spination, a pair of sphenotic spines on the head, and nine or so elongated dorsal rays. They differ in several interesting respects. *C. fimbriata* transforms at a much smaller size, 14.0 mm, whereas the Pacific species can attain a length of at least 32 mm before transformation. The opercular spination is more strikingly developed on the Pacific form, and the pelvic fins become markedly more elongate, extending almost to the base of the caudal fin, whereas the fins attain only about 40% of this length proportionately in *C. fimbriata.*

***Engyrophrys sancti-laurentii* (Jordan and Bollman)**
(3 occurrences, 3 larvae)

Only three larvae of this species were obtained on ETP II, two from the vicinity of the Gulf of Panama and one from near Puntarenas, Costa Rica.

***Monolene* sp.**
(1 occurrence, 1 larva)

A 16-mm specimen was obtained at Station 47.520. Larvae of *Monolene* develop a single, prominent elongated dorsal ray (2nd fin ray)—this ray was 6 mm long. Its meristics—D.82, A.63, Vert. 39—would fit *Monolene asaedai* Clark (Perkins, 1963) and possibly *M. dubiosa* Garman. The other two eastern Pacific species, *M. maculipinna* Garman and *M. danae Bruun*, have higher fin ray counts. Morrow (1957b) reported taking a 65-mm larva of *M. maculipinna* off Peru in a pelagic trawl fishing to 152-fm depth over rather deep water (1,300 fm). Morrow's specimen had the following meristics: D.98, A.79, Vert. 43. *Monolene danae* Bruun (1937) was described from a juvenile taken in a pelagic trawl off Panama by the *Dana* in 1922.

***Syacium ovale* (Günther)**
(55 occurrences, 480 larvae)

Although larvae of *S. ovale* were the most common bothid flatfish collected on both ETP I and ETP II, it was decidedly more abundant in ETP II as compared with ETP I (24 occurrences, 84 larvae). Larvae of *Syacium* occurred in a broad coastal band between Manzanillo, Mexico, and Ecuador (Figure 3); only three collections were obtained to the south of the

TABLE 23.—Familial composition of Lophiiform larvae taken on the second multivessel EASTROPAC survey, summarized by vessel pattern.

Family	*Washington* 45.000 series		*Undaunted* 46.000 series		*Rockaway* 47.000 series		Total EASTROPAC II	
	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae	No. positive hauls	No. larvae
Caulophrynidae	0	0	2	2	0	0	2	2
Centrophrynidae	1	1	0	0	0	0	1	1
Ceratiidae	0	0	2	3	3	5	5	8
Gigantactinidae	8	9	5	5	5	13	18	27
Himantolophidae	4	5	1	1	3	3	8	9
Linophrynidae	2	2	0	0	19	32	21	34
Melanocetidae	3	3	13	18	17	23	33	44
Oneirodidae	11	11	13	18	23	53	47	82
Unidentified ceratioids	9	11	7	7	10	16	26	34
Antennariidae	0	0	1	1	0	0	1	1
Lophiidae	0	0	1	1	0	0	1	1
Total Lophiiform	25	42	33	56	56	145	114	243

equator. Most larvae of *Syacium* were under 5 mm in standard length, and few were as large as 9 mm. At the latter size, the adult complement of fin rays were present in all fins except the pectoral, and the vertebral column was completely ossified. The vertebral count in specimens examined was 10 + 25.

54. CYNOGLOSSIDAE

(56 occurrences, 362 larvae)

Larvae of *Symphurus* spp. were taken in a broad coastal band between Manzanillo, Mexico, and northern Peru. *Symphurus* larvae were taken in slightly less hauls than on ETP I (56 versus 63 occurrences), but in slightly larger numbers (362 versus 304 larvae). Two kinds of *Symphurus* larvae were widely distributed, and three or four additional kinds occurred sparingly. Of the two common forms, one developed two elongated dorsal rays and the other six elongated dorsal rays.

56. LOPHIIFORMES

(114 occurrences, 243 larvae)

Lophiiform larvae were accumulated during the identification and enumeration of ETP II larvae, and then studied as a unit. Ten families were represented (Table 23). All but two of the specimens belonged to the subfamily Ceratioidei, a group of fishes whose ontogeny and taxonomy were dealt with in the impressive contribution of Bertelsen (1951). Ceratioid fishes have the most striking sexual dimorphism found in fishes. The males are parasitic in some ceratioids, free-living in others, but always quite small. Bertelsen showed that sex can be determined in the late larval stage; a papilliform illicium develops on the head of the female, but not on the male. A major achievement of Bertelsen was defining the distinguishing characteristics of larvae of all 10 ceratioid families. His work makes it possible to identify larger ceratioid larvae to the family level with assurance; however, small ceratioid larvae are much more difficult to identify because they have few distinguishing characters. Although Bertelsen worked out life history series to the generic or species level within all ceratioid families, ontogeny of the less common genera and species still remains unknown.

The ceratioids are a particularly difficult group in which to work out new developmental series. These cannot be based on larvae alone but must include transforming and adolescent specimens, preferably of both sexes, as well as adults. The EASTROPAC material, almost exclusively larvae, is inadequate for this purpose. Distributions of larvae are shown for five ceratioid families (Figure 18), as noted in the discussion of families. Most kinds of ceratioid larvae are quite rotund, hence aptly described as butterballs.

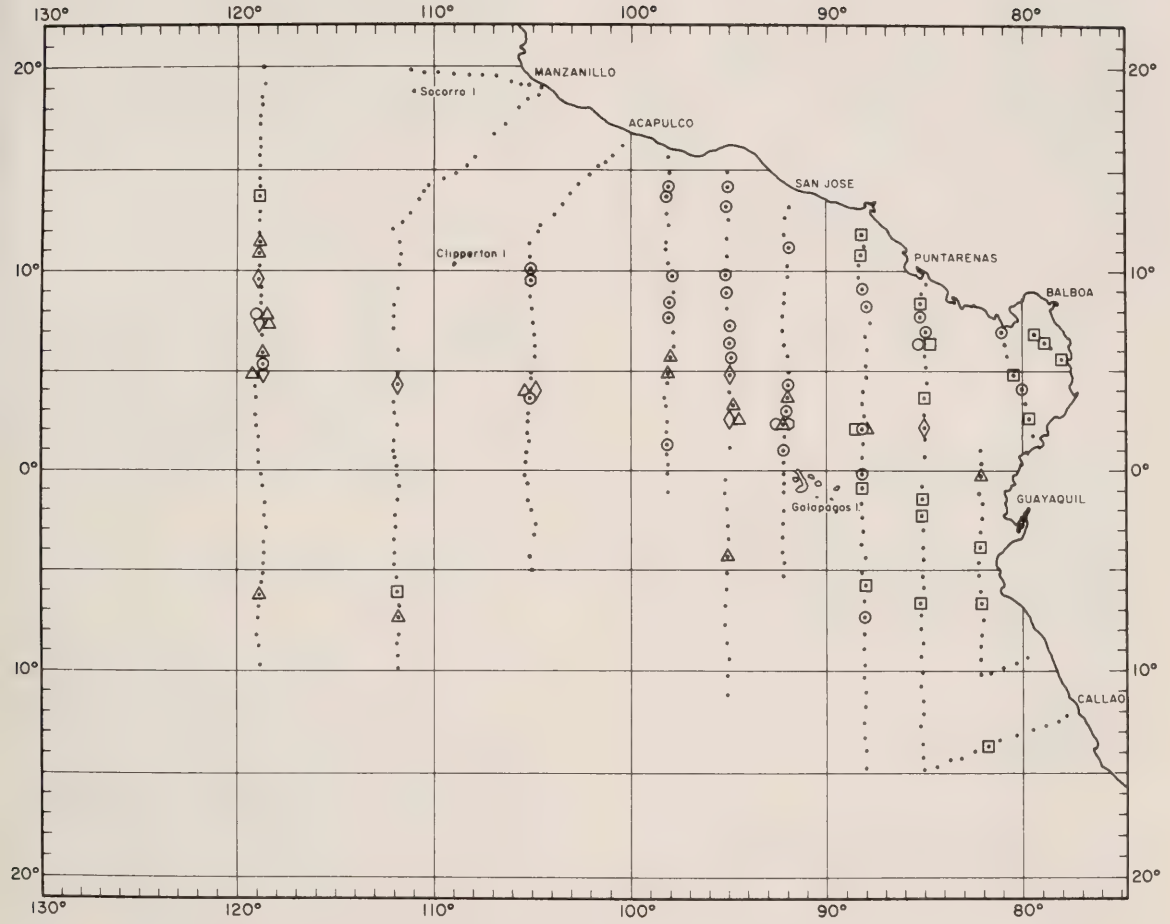

FIGURE 18.—Distribution of larvae of the lophiiform families Caulophrynidae (*Caulophryne jordani*) (open hexagon with dot), Gigantactinidae (*Gigantactis* sp.) (open triangle with dot), Himantolophidae (*Himantolophus* sp.) (open diamond with dot), Linophrynidae (2 or more genera represented) (open square with dot), and Melanocetidae (*Melanocetus* spp.) (open circle with dot); negative hauls are shown as small solid circles.

Caulophrynidae
(2 occurrences, 2 larvae)

Bertelsen referred all material of Caulophrynidae to a single species, *Caulophryne jordani* Goode and Bean. This is the only ceratioid fish known to develop pelvic fins. The two occurrences (Figure 18) were north of the equator in the pattern occupied by the middle vessel.

Centrophrynidae
(1 occurrence, 1 larva)

A single specimen was obtained of *Centrophyrne spinulosa* Regan and Trewavas in the offshore pattern (Station 45.325). Larvae of this species develop a digitiform barbel on the throat, a character unique to the species.

Ceratiidae
(5 occurrences, 8 larvae)

Larvae were obtained of two species of Ceratiidae, *Cryptopsaras couesi* Gill and *Ceratias holboelli* Kroyer. Bertelsen had previously recorded larvae of *C. couesi* from the eastern tropical Pacific, but not of *C. holboelli*. Ceratiid larvae are peculiarly "humpbacked," and the larger larvae of females develop "caruncles" on their backs. The caudal ray count in ceratioid fishes is constant at nine, except for two species that develop only eight caudal rays—*C. couesi* is one of these.

Gigantactinidae
(18 occurrences, 27 larvae)

Larvae of *Gigantactis* sp. were taken in a triangular-shaped wedge, broadest offshore (Figure 18). Even small larvae of this family can be identified with certainty, because of the large size of the pectoral fins.

Himantolophidae
(8 occurrences, 9 larvae)

Larvae of Himantolophidae were taken to the north of the equator, between lat 2° and 10°N in all vessel patterns (Figure 18). Larvae are similar to Bertelsen's series for *Himantolophus groenlandicus* Reinhardt, and he recorded specimens from Panama. Two additional species of *Himantolophus* have been described from Panama or vicinity: *H. azuerlucens* Beebe and Crane and *H. rostratus* Regan. I have recorded the EASTROPAC larvae simply as *Himantolophus* sp.

Linophrynidae
(21 occurrences, 34 larvae)

Several kinds of linophrynid larvae were taken, of which three were common—larvae of *Borophryne apogon* Regan, of the *Linophryne macrorhinus* group, and of the type designated by Bertelsen as "*Hyaloceratis*." All but two occurrences of linophrynid larvae were in the inner pattern shoreward of the Galapagos Islands (Figure 18). Most linophrynid larvae are more elongate than other ceratioid larvae and also have the lowest D and A counts, usually D3 and A3.

Melanocetidae
(33 occurrences, 44 larvae)

At least two kinds of *Melanocetus* larvae were obtained on ETP II, with most specimens referable to *M. polyactis* Regan and the remainder to *M. johnsoni* Günther. Most records of *Melanocetus* were from the northeast quadrant of the EASTROPAC pattern (Figure 18).

Oneirodidae
(47 occurrences, 82 larvae)

At least one-third of the ceratioid larvae taken on ETP II were referable to the family Oneirodidae. Bertelsen (1951) recorded seven kinds of oneirodid larvae belonging to six genera from collections made off Panama. All but one of these were taken in ETP II, together with a new record for the eastern Pacific. Oneirodid larvae sampled on ETP II included *Chaenophryne draco*-group, *Chaenophryne longiceps*-group, *Dolopichthys* sp., *Micropolichthys microlophus* (Regan), *Oneirodes eschrichti*-group, *Oneirodes melanocauda* Bertelsen, and *Pentherichthys* sp. Bertelsen could identify some oneirodid larvae only to species groups, including the three listed above. Bertelsen included 24 nominal species in the *Oneirodes eschrichti*-group, most of which were possibly synonyms.

Perhaps the most interesting record of an oneirodid larva from ETP II was of *Oneirodes melanocauda* from Station 47.008, off Panama. A male, 9.5 mm TL (6.5 mm SL), agreed in all essential characters with Bertelsen's description. This is one of the more heavily pigmented ceratioid larvae. The fin counts were D6, A4, P19, C9. Bertelsen based his description of *O. melanocauda* on four specimens, 8 to 21 mm TL, the

largest a metamorphosing female. These were obtained in the South China Sea, Indian Ocean, and Caribbean Sea. The EASTROPAC record is the first from the Pacific.

The caudal fin is usually unpigmented in ceratioid larvae, but caudal pigment is developed on several kinds of oneirodid larvae. Larvae of *O. melanocauda* have stippled pigment near the outer margin of the caudal rays. Larvae of *Penthrichthys* sp. have pigment sprinkled over much of the caudal fin rays. A third kind of oneirodid larva with streaks of caudal pigment between the rays was taken at Station 47.250 (ontogenetic series yet to be worked out).

The larvae of *Pentherichthys* from the eastern Pacific are probably referable to *P. atratus* (Regan and Trewavas). Collections were made at six stations in the inner pattern between lat 2° and 8°N. The 10 specimens ranged in total length from 3.2 to 7.0 mm. Bertelsen remarked on the paucity of small specimens of *Pentherichthys* in the *Dana* material; only 2 of 19 specimens were under 7.5 mm in total length.

Antennariidae
(1 occurrence, 1 larva)

The specimen, taken at an inshore Station, 46.132, on the middle pattern, was 7.5 mm SL and had fin counts of D-II + I-13, A7, P10, V5, C9. These counts could apply equally to species in the genera *Histrio* or *Antennarius*.

Lophiidae
(1 occurrence, 1 larva)

A specimen of a lophiid larvae was obtained in the middle pattern at Station 46.145. This specimen, 15.5 mm SL (25.0 mm TL), had the following counts: D-II + I + III — 8, A6, P16/17, V6, C8. This specimen is referable to the genus *Lophiomus*. Garman described two species of *Lophiomus* from the eastern Pacific with identical counts to the above. Norman in his unpublished synopsis considered the genus monotypic with Garman's species as junior synonyms of *L. setigerus* Vahl. The third dorsal spine is rather widely separated from an anterior group of two spines and a posterior group of three. The last ray in both the dorsal and anal fins was bifurcate to the base, differing in this respect from the last ray in ceratioid fishes, which is single. The larvae had two spines above the eye on either side of the head, differing in this character from the published larval series for *Lophius piscatorius* and *L. americanus* (Tåning, 1923); the pectoral fins were considerably smaller and compact.

57. OTHER IDENTIFIED
(23 occurrences, 51 larvae)

Two of the families, Amarsipidae and Stromateidae, have been discussed in the section dealing with Nomeidae and other Stromateiodei (No. 42). Other families included under "other identified" include Eutaeniophoridae (2 occurrences, 2 larvae), Gadidae (7 occurrences, 10 larvae), Callionymidae (2 occurrences, 2 larvae), Fistulariidae (1 occurrence, 1 larva), Gerridae-*Eucinostomus* sp. (4 occurrences, 15 larvae), Microdesmidae (4 occurrences, 6 larvae), Pomadasyidae-*Anisotremus* sp. (2 occurrences, 7 larvae), and Tetradontidae (1 occurrence, 1 larva).

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APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).

STATION NUMBER	Myctophidae	Gonostomatidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Bathylagidae	Paralepididae	Scopelarchidae	Melamphaidae	Bregmacerotidae	Exocoetidae	Trachypteridae	Apogonidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
45.016	12	14	.	.	.	2	.	2	2	2	.	.	.	.	.	.	.	.	.	.	2	1	37
45.018	35	86	2	.	2	1	.	3	2	.	.	.	.	.	.	2	1	.	.	2	.	.	136
45.020	14	5	3	.	1	1	.	.	.	.	4	.	.	.	.	.	.	1	.	1	.	1	31
45.021	13	17	2	.	1	6	.	3	.	1	4	.	.	.	.	3	1	.	.	2	.	1	54
45.023	61	106	.	.	.	3	.	2	.	2	8	.	.	.	.	1	2	1	.	2	1	.	189
45.024	86	96	1	.	1	3	.	3	.	2	2	.	.	.	.	.	1	1	.	3	.	5	204
45.026	40	30	.	.	9	.	4	4	.	10	3	.	.	.	.	.	2	3	1	2	2	2	112
45.028	24	22	.	.	2	5	9	4	3	1	3	.	.	.	.	.	.	8	.	1	1	1	84
45.030	34	60	.	.	8	.	.	2	1	2	.	.	.	.	.	.	.	9	.	2	.	3	121
45.032	158	111	.	.	14	1	7	3	1	12	5	.	.	.	.	2	2	17	.	10	.	10	353
45.034	146	37	.	.	8	2	1	1	4	2	9	.	.	.	.	1	.	1	.	1	2	9	224
45.035	40	29	.	.	7	.	2	.	3	4	4	1	.	.	.	.	.	9	.	3	4	1	107
45.037	41	25	1	.	18	4	10	1	.	2	11	.	.	.	.	1	.	2	.	1	4	3	124
45.039	77	82	.	.	7	3	1	4	12	4	11	.	.	.	.	2	.	2	.	5	5	1	216
45.041	29	49	.	.	2	4	8	1	4	4	9	.	.	.	.	.	.	1	.	.	10	1	122
45.043	17	16	.	.	2	.	5	3	1	5	4	.	.	.	.	1	.	6	.	3	3	1	67
45.044	50	41	1	.	3	.	4	4	5	2	4	.	.	.	.	.	.	4	.	1	3	5	127
45.046	43	57	23	.	43	.	2	1	6	6	8	.	.	.	1	5	2	5	.	2	.	1	205
45.048	25	21	12	.	9	.	2	1	1	6	1	2	.	.	1	1	1	3	.	2	.	4	92
45.050	19	3	6	.	1	.	1	2	.	2	.	.	.	.	.	.	.	1	.	2	2	1	40
45.051	87	15	14	.	.	.	4	1	.	.	1	.	.	.	.	.	1	.	.	2	.	.	125
45.053	75	19	31	.	.	.	.	2	.	3	11	.	.	2	1	.	.	.	.	4	.	3	151
45.054	44	3	16	1	.	.	1	.	.	4	24	.	.	1	.	.	.	.	.	1	1	1	97
45.056	22	6	20	.	.	.	.	1	.	2	23	.	1	.	.	.	2	1	.	5	.	7	90
45.058	146	18	13	.	2	1	1	6	.	2	11	.	1	11	1	.	.	.	.	8	2	5	228
45.060	82	4	2	.	5	8	1	3	2	5	29	.	.	13	1	.	.	1	.	3	2	7	168
45.063	29	46	2	.	2	14	1	3	.	.	9	.	.	10	2	2	2	.	.	6	1	1	138
45.065	116	374	9	.	6	26	.	25	.	.	1	.	.	29	1	2	3	5	3	11	.	23	634
45.067	185	584	37	9	2	48	3	56	.	.	.	.	1	12	3	.	1	5	1	31	3	11	992
45.071	42	40	7	.	.	3	.	5	.	.	2	.	.	11	1	.	1	3	.	5	.	1	121
45.073	65	68	14	.	.	2	2	5	.	.	1	.	.	22	.	.	.	3	.	4	1	16	203
45.078	71	107	10	.	.	.	1	6	2	.	3	.	.	3	1	.	.	4	.	2	.	2	212
45.083	37	26	13	.	.	1	.	5	.	1	.	.	.	11	.	.	2	4	.	1	.	4	105
45.086	65	77	2	1	.	2	3	9	.	5	3	.	.	1	.	.	.	2	.	.	.	21	191
45.090	47	67	3	1	.	3	8	5	.	.	.	.	.	1	.	1	.	2	.	6	.	12	156
45.094	150	107	12	.	.	3	6	27	.	.	1	.	.	2	.	2	1	2	.	.	.	33	346
45.098	43	16	3	.	.	.	2	8	.	1	.	.	.	1	.	.	1	.	.	.	.	10	85
45.102	136	82	12	.	.	5	1	24	.	7	.	.	.	2	.	1	.	1	.	1	.	16	288
45.106	265	21	21	.	.	2	5	4	1	5	.	1	.	.	.	1	.	2	.	1	3	22	354
45.110	545	32	188	.	.	5	12	5	1	4	.	.	.	.	.	7	.	5	.	4	.	1	817
45.114	40	20	51	.	.	.	2	2	.	1	.	.	.	.	.	.	.	5	.	.	1	16	138
45.117	92	49	86	.	.	.	1	4	.	2	.	.	.	.	.	.	.	6	.	2	1	20	263
45.121	55	98	209	.	.	.	4	3	.	2	.	.	.	1	.	.	.	.	.	2	.	25	399
45.125	41	325	39	.	.	.	.	1	.	1	.	.	.	.	1	.	.	6	.	2	.	.	416
45.127	21	39	31	.	.	.	.	.	.	6	.	.	.	7	2	.	.	.	.	3	3	10	122
45.129	22	3	24	.	.	.	.	.	.	4	.	.	.	3	.	.	.	.	.	.	1	1	63
45.131	73	337	23	.	.	.	.	.	.	2	.	.	.	2	1	.	.	2	.	3	4	25	472
45.133	323	33	23	.	9	4	.	5	5	.	7	.	.	.	.	.	.	.	1	3	.	3	416
45.135	165	17	19	.	2	.	.	2	1	.	3	2	.	.	.	.	.	.	1	1	4	10	227
45.137	11	.	12	1	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	27
45.139	24	2	3	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	3	36
45.146	106	87	49	8	.	.	.	11	10	1	.	.	.	.	.	.	.	.	.	2	20	44	338

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Myctophidae	Gonostomatidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Bathylagidae	Paralepididae	Scopelarchidae	Melamphaidae	Bregmacerotidae	Exocoetidae	Trachypteridae	Apogonidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
45.163	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
45.165	152	65	212	1	6	3	.	1	4	2	8	.	.	.	.	.	.	.	.	3	2	12	471
45.167	86	6	10	.	.	.	.	.	2	2	.	.	.	.	2	.	.	1	.	.	.	10	119
45.169	56	15	1	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	8	82
45.171	26	1	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	9	50
45.173	10	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13
45.175	62	27	29	.	.	.	.	1	.	.	.	.	.	1	1	.	.	1	.	2	.	3	127
45.177	70	145	46	.	.	.	.	5	.	.	.	.	.	.	1	.	.	7	.	3	.	1	281
45.179	59	33	8	.	.	.	.	1	1	1	.	.	.	.	.	.	.	1	.	.	.	9	113
45.183	26	14	70	.	.	.	4	4	.	2	.	.	.	.	.	.	.	.	.	1	.	2	123
45.187	255	14	87	.	.	.	16	3	.	2	.	.	.	.	.	.	.	.	.	3	.	2	382
45.191	144	15	80	.	.	.	5	17	.	5	.	.	.	.	.	1	.	.	.	1	.	4	272
45.194	49	4	40	.	.	.	3	11	.	1	.	.	.	.	.	.	.	1	.	.	.	4	113
45.198	251	21	31	.	.	3	7	22	.	1	.	.	.	.	.	1	.	.	.	2	.	11	350
45.202	53	19	5	.	.	1	2	9	.	1	.	.	.	.	.	.	.	.	.	2	.	.	92
45.206	22	3	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	30
45.283	102	13	7	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	3	129
45.287	25	82	1	.	.	.	2	3	.	.	.	.	.	.	.	.	.	.	.	.	1	.	114
45.289	157	125	1	.	.	.	2	16	.	1	.	.	.	.	.	1	.	.	.	1	.	2	306
45.293	157	58	13	.	2	4	4	11	1	2	2	.	1	2	1	1	.	.	.	2	2	2	265
45.297	231	107	14	.	1	15	7	17	2	6	11	.	.	19	.	.	1	.	.	.	1	8	440
45.301	24	26	13	.	.	4	8	5	.	.	3	.	1	2	.	1	1	1	.	4	.	.	93
45.305	119	1040	17	.	1	3	2	.	1	1	6	.	1	.	.	.	6	10	.	1	.	9	1217
45.309	44	150	22	1	1	8	.	4	1	1	2	.	.	3	.	.	3	2	.	2	.	7	251
45.313	49	35	5	.	1	4	2	6	.	.	2	.	.	4	.	.	1	.	.	1	.	9	119
45.316	41	34	8	1	.	3	1	2	.	1	4	.	.	.	1	.	.	.	.	1	.	2	99
45.319	32	46	17	.	.	2	.	3	.	3	4	.	.	1	.	.	.	.	.	2	.	1	111
45.321	45	13	20	.	.	.	2	.	.	7	4	.	.	.	.	.	.	.	.	1	1	1	94
45.323	51	4	1	.	.	3	1	2	.	7	1	.	.	.	.	1	.	.	.	1	1	1	74
45.325	1002	28	19	.	1	.	42	3	1	7	1	.	1	.	6	.	1	1	1	4	.	3	1128
45.329	69	4	11	.	8	.	3	1	.	3	.	1	.	.	1	.	1	4	.	1	.	3	110
45.331	235	5	11	.	1	1	13	.	.	6	3	.	.	.	1	.	.	10	.	1	2	1	290
45.333	108	28	10	.	.	2	5	1	.	4	3	1	.	.	.	.	1	25	.	13	.	.	201
45.335	65	32	2	.	14	5	8	3	3	1	1	.	.	.	.	.	1	9	.	8	1	2	155
45.337	49	12	6	.	21	12	1	3	1	12	6	.	.	.	.	2	2	14	.	1	.	16	158
45.339	26	8	.	.	15	4	2	.	.	7	8	1	.	.	.	3	1	5	.	9	2	9	100
45.341	47	70	.	.	7	1	3	4	4	3	2	.	.	.	.	.	1	1	.	1	.	.	144
45.343	17	32	.	.	8	1	2	2	.	2	2	3	.	.	.	.	1	4	.	2	.	1	77
45.344	21	37	.	.	6	2	1	3	1	3	3	1	1	.	.	.	1	11	.	4	.	4	99
45.346	19	19	.	.	2	1	.	4	.	3	2	.	.	.	.	.	1	4	.	2	.	1	58
45.348	30	120	.	.	3	.	.	4	4	.	.	.	.	.	.	.	.	2	.	3	.	.	166
45.350	70	297	.	.	1	2	.	1	.	.	.	.	.	.	.	.	.	6	.	1	.	5	383
45.352	29	66	.	.	.	.	3	2	.	1	1	1	.	.	.	.	.	3	.	.	.	10	116
45.356	69	153	.	.	5	.	11	6	1	1	.	3	.	.	.	.	2	19	9	1	2	.	282
45.358	98	107	.	.	1	.	1	.	.	4	2	4	1	.	.	.	1	6	5	2	3	7	242
45.360	18	37	.	.	.	1	7	2	.	1	.	.	.	.	.	.	.	9	5	4	3	4	91
45.362	36	31	.	.	.	.	6	8	.	4	2	.	.	.	.	.	1	8	6	17	8	1	128
45.365	99	55	.	.	.	.	1	1	.	.	27	.	.	.	.	.	.	.	4	103	15	6	311
45.367	23	10	.	.	1	1	7	1	.	.	3	.	.	.	.	.	.	.	.	19	.	73	138
45.369	101	106	.	.	.	2	3	10	1	2	25	.	.	.	.	.	1	7	12	61	11	15	357
45.371	120	239	.	.	1	2	13	4	3	10	13	.	1	.	.	.	.	7	6	10	6	11	446
45.373	117	149	.	.	1	.	14	1	.	2	.	2	.	.	.	.	.	13	9	10	3	.	321

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Myctophidae	Gonostomatidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Bathylagidae	Paralepididae	Scopelarchidae	Melamphaidae	Bregmacerotidae	Exocoetidae	Trachypteridae	Apogonidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
45.375	34	39	.	.	.	1	3	1	.	1	2	2	.	.	.	.	.	2	.	4	.	2	91
45.377	67	86	.	.	.	2	8	3	1	3	1	.	.	.	.	.	2	18	6	11	.	18	226
45.379	199	805	.	.	.	1	2	6	2	3	3	1	.	.	.	.	.	3	.	10	12	1	1048
45.381	98	248	.	.	1	.	4	3	.	2	3	.	.	.	.	.	.	2	.	3	2	5	371
45.383	40	20	.	.	.	.	4	.	.	4	.	.	.	.	.	.	.	.	.	2	5	3	78
45.385	19	60	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	83
45.387	26	429	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	461
CRUISE	46																						
46.002	14	19	.	.	.	.	2	1	.	.	.	2	.	.	.	.	1	14	.	2	2	1	58
46.004	103	122	.	.	11	3	4	18	2	5	3	.	.	.	.	.	7	21	2	3	2	3	309
46.006	30	19	.	.	5	1	1	2	.	1	5	.	1	.	.	1	.	9	.	1	4	1	81
46.007	10	28	.	.	1	.	.	2	.	4	1	.	.	.	.	.	.	14	.	1	.	6	67
46.009	17	23	.	.	2	.	1	2	.	.	1	.	.	1	.	.	2	8	.	2	.	3	62
46.011	60	72	.	.	4	2	1	5	3	5	1	1	.	.	.	1	3	16	.	2	1	.	177
46.013	89	51	.	.	2	5	.	2	5	1	2	.	.	.	.	.	1	7	.	1	.	.	166
46.015	18	17	.	.	2	.	1	11	.	4	7	.	.	.	.	.	1	8	.	1	.	.	70
46.017	25	4	.	.	11	.	5	.	1	1	9	.	.	.	.	.	2	1	.	2	1	.	62
46.019	285	148	.	.	17	2	1	2	9	1	9	.	1	1	.	.	2	.	.	3	.	.	481
46.020	160	80	.	.	16	2	10	3	4	2	2	1	.	.	.	.	2	1	1	.	1	.	285
46.022	38	14	11	.	4	.	1	2	1	8	1	2	.	.	1	1	1	8	3	1	1	2	100
46.024	64	27	2	.	3	1	5	1	3	2	2	1	.	.	2	.	.	7	1	2	2	.	125
46.026	206	140	2	.	2	.	5	6	4	11	3	1	.	1	.	4	.	13	3	.	2	.	403
46.028	412	157	10	.	9	2	12	6	1	10	4	.	.	.	1	.	3	15	2	2	1	8	655
46.030	85	7	12	.	3	2	8	.	.	2	2	.	.	.	.	.	1	2	.	.	.	7	131
46.032	9	.	8	.	.	.	1	.	.	.	.	.	.	.	.	1	.	1	.	1	.	.	21
46.034	152	40	17	1	.	3	5	3	1	1	9	.	.	.	1	1	1	1	.	7	2	3	248
46.036	436	127	28	.	2	1	7	8	1	4	4	1	.	1	.	1	3	.	1	3	.	6	634
46.038	20	7	10	.	.	.	3	1	1	2	.	1	.	.	.	.	.	1	.	.	.	3	49
46.040	25	29	8	.	.	1	.	4	.	1	.	.	.	1	2	.	.	.	.	3	.	4	69
46.042	62	133	5	.	1	.	4	.	.	2	1	2	.	1	.	.	.	.	1	1	1	4	218
46.044	89	96	21	.	.	1	1	1	.	5	1	1	.	1	.	.	.	1	.	1	2	11	232
46.046	78	57	22	.	.	2	1	2	3	3	.	.	.	2	1	.	.	.	1	8	.	11	191
46.048	63	54	24	.	1	.	10	3	.	5	4	1	.	4	1	.	1	.	.	3	3	4	181
46.050	250	184	15	.	.	1	12	24	1	7	11	.	.	11	1	1	.	4	.	3	4	15	547
46.052	319	217	23	.	3	.	7	18	1	3	4	.	.	11	1	.	1	2	.	13	3	5	631
46.054	211	181	22	.	.	3	20	23	1	6	9	.	.	.	.	2	.	.	.	2	3	14	497
46.055	100	73	10	.	1	1	5	18	4	4	4	.	.	3	3	4	.	3	.	.	.	16	249
46.057	751	649	3	.	.	2	10	70	2	3	.	.	.	2	.	3	.	3	.	6	2	.	1506
46.059	494	504	.	.	.	5	2	59	2	1	1	.	.	.	.	1	.	2	.	22	.	5	1098
46.061	148	98	5	1	.	1	3	23	.	1	.	.	.	.	.	.	.	.	.	14	.	72	366
46.063	48	19	8	3	.	.	2	10	.	.	.	.	.	.	.	.	.	1	.	.	5	20	116
46.065	404	97	14	.	.	5	4	50	.	2	.	.	.	.	.	6	.	.	.	2	.	8	592
46.067	269	121	20	.	.	2	5	18	.	1	.	.	.	.	.	.	.	.	.	2	3	20	461
46.069	116	55	23	.	.	.	22	53	.	4	.	.	.	.	.	.	.	.	.	5	33	20	331
46.071	72	27	34	.	.	.	14	22	.	.	.	.	.	.	.	.	.	.	.	4	3	16	192
46.075	35	21	32	.	.	.	5	17	.	4	.	.	.	.	.	.	.	.	.	.	.	6	120
46.077	36	19	12	.	.	1	1	3	.	1	.	.	1	1	.	1	.	.	.	3	.	.	79
46.079	408	30	14	.	.	22	23	31	.	2	.	.	.	.	.	.	.	1	.	4	.	1	536
46.082	61	46	13	.	.	5	17	15	.	2	.	.	.	.	.	.	.	1	.	8	.	8	176

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Myctophidae	Gonostomatidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Bathylagidae	Paralepididae	Scopelarchidae	Melamphaidae	Bregmacerotidae	Exocoetidae	Trachypteridae	Apogonidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
46.084	45	39	13	.	.	2	21	21	.	3	.	.	.	.	.	.	.	.	.	6	1	8	159
46.086	102	233	25	.	1	2	33	26	.	3	.	.	.	.	.	.	.	4	.	8	.	1	443
46.088	124	60	16	.	.	6	8	27	.	.	.	.	.	.	.	.	.	3	.	4	1	9	258
46.090	99	24	47	.	1	6	4	28	3	6	.	.	.	.	.	1	.	7	.	.	.	143	369
46.092	100	29	36	.	.	4	3	10	2	4	.	.	.	1	.	.	1	4	.	.	4	2	200
46.094	300	156	87	.	2	7	3	21	.	8	3	.	2	.	.	1	.	.	.	3	1	1	595
46.096	240	249	54	.	3	2	13	24	1	5	3	3	.	7	.	.	3	2	.	7	8	4	628
46.098	73	42	35	.	.	8	2	4	.	3	.	.	.	7	1	1	.	1	.	2	3	15	197
46.100	125	8	41	.	3	.	2	1	3	2	9	.	.	.	.	.	.	.	.	1	1	6	202
46.102	334	56	69	1	1	4	3	10	.	9	7	.	.	1	.	2	.	.	.	4	3	4	508
46.104	109	48	36	1	2	4	.	10	1	1	.	.	.	2	.	.	1	2	.	2	1	12	232
46.106	115	41	19	.	.	1	9	1	.	2	.	1	1	.	.	.	2	7	1	2	4	4	210
46.108	250	38	45	.	.	7	27	.	.	.	.	.	.	.	.	.	.	20	4	5	1	18	415
46.110	162	10	22	.	1	.	5	.	5	3	.	1	.	.	.	.	.	2	3	15	1	.	230
46.112	562	75	14	.	1	1	16	3	.	.	.	.	.	.	.	.	.	3	14	49	.	.	738
46.114	31	6	2	.	1	1	3	.	2	.	3	2	.	.	.	.	.	3	.	7	.	.	61
46.116	14	5	3	.	1	.	.	1	.	3	.	.	.	.	.	.	.	7	.	1	.	2	37
46.118	176	85	6	.	8	1	3	7	2	5	1	1	1	.	.	.	4	13	.	1	4	3	321
46.120	80	100	.	.	13	2	1	9	1	1	2	1	3	.	.	.	2	12	.	10	.	.	237
46.122	17	29	.	.	2	2	4	4	2	2	3	.	1	.	.	.	1	10	.	8	.	.	85
46.124	19	22	.	.	.	.	2	3	1	4	3	.	.	.	.	.	1	12	.	6	3	3	79
46.126	63	98	.	.	13	1	10	7	1	7	1	1	1	.	.	.	.	4	.	20	10	.	237
46.128	113	131	.	.	11	9	8	11	2	9	19	.	.	.	.	.	1	12	.	7	7	3	343
46.130	46	53	.	.	1	5	11	6	1	6	10	.	.	.	.	.	1	9	.	5	20	9	183
46.132	26	26	.	.	.	.	5	9	.	.	4	.	.	.	.	.	.	17	11	12	19	1	130
46.134	9	12	.	.	3	.	8	.	.	.	511	.	.	.	.	.	2	.	20	93	18	8	684
46.135	81	12	.	.	1	.	8	.	.	.	927	.	.	.	.	.	1	5	6	149	24	4	1218
46.137	201	28	1	.	1	1	24	.	.	7	9	.	.	.	.	.	.	4	.	278	.	7	561
46.139	175	52	1	.	1	.	11	1	1	6	1	.	.	.	.	.	.	15	3	15	.	1	283
46.141	438	20	4	1	1	2	18	1	1	4	.	4	1	.	2	.	1	6	.	8	3	3	518
46.143	113	15	30	.	1	.	10	.	1	2	1	.	.	.	1	.	.	7	1	3	2	5	201
46.145	282	119	24	.	3	2	38	3	.	2	.	.	1	.	.	.	2	4	2	4	2	1	489
46.147	484	41	49	.	2	1	41	1	3	4	.	.	.	.	.	.	.	5	1	4	.	6	642
46.149	1333	14	30	.	1	10	22	.	.	7	1	.	.	.	.	.	.	6	.	4	2	2	1432
46.151	1358	9	24	.	1	4	13	.	.	8	.	.	.	.	.	2	.	.	.	1	.	.	1420
46.153	2561	165	81	.	2	3	4	.	1	7	.	1	1	.	.	.	.	4	.	18	.	16	2864
46.155	973	148	67	.	4	9	6	1	.	8	1	.	.	.	2	1	2	3	3	11	.	3	1234
46.157	490	27	78	1	1	7	6	5	1	8	3	.	1	7	2	.	2	.	.	7	2	12	660
46.159	71	11	32	.	.	2	2	1	.	2	.	.	.	3	1	.	2	.	.	6	.	1	134
46.161	350	47	73	.	4	2	8	12	2	15	.	.	.	.	.	1	.	.	1	12	1	3	531
46.163	290	88	64	.	7	4	10	12	1	13	.	.	1	1	.	.	.	.	.	6	2	41	540
46.165	90	36	60	.	5	.	18	15	.	7	.	3	1	1	.	1	1	.	.	9	5	9	261
46.167	195	40	49	.	3	1	37	7	.	11	.	.	2	2	.	.	.	5	.	7	2	25	386
46.169	163	236	30	.	.	4	52	46	.	10	.	1	.	.	.	2	.	1	.	4	4	10	563
46.171	255	55	15	.	1	0	44	28	.	7	.	.	.	.	.	.	.	.	.	72	.	60	545
46.173	33	15	6	.	.	.	10	6	.	1	.	.	.	.	.	.	.	.	.	5	.	2	78
46.175	52	76	4	.	1	.	21	3	.	2	.	.	.	.	.	.	.	.	.	2	.	1	162
46.177	124	33	17	.	1	2	45	16	.	10	.	.	.	.	.	.	.	.	1	26	.	6	281
46.179	213	110	54	.	1	4	135	19	.	22	.	.	.	.	.	.	.	.	3	110	3	14	688
46.181	52	58	13	3	2	8	132	13	.	14	.	.	.	.	.	.	.	1	.	21	18	4	339
46.183	85	21	29	2	4	11	47	11	1	9	2	.	.	.	.	2	.	2	.	5	.	4	235
46.185	262	97	54	.	2	10	45	12	.	9	.	.	.	.	.	3	.	2	.	6	.	3	505

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Myctophidae	Gonostomatidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Bathylagidae	Paralepididae	Scopelarchidae	Melamphaidae	Bregmacerotidae	Exocoetidae	Trachypteridae	Apogonidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
46.187	516	42	23	.	1	1	17	7	2	2	.	.	.	.	1	.	.	2	.	6	3	6	629
46.189	236	5	19	1	.	1	8	.	1	4	.	.	.	.	.	.	.	.	.	1	1	1	278
CRUISE	47																						
47.001	97	63	6	.	.	.	4	2	.	2	15	.	.	.	1	.	1	1	.	42	.	.	234
47.005	287	206	21	.	3	.	6	6	1	8	22	.	.	1	.	.	1	2	.	81	6	17	668
47.008	257	49	5	.	9	2	7	2	3	13	4	.	.	.	.	.	.	.	.	70	1	7	429
47.011	161	26	4	.	2	1	3	1	1	5	21	.	.	.	.	.	.	2	.	32	2	2	263
47.019	370	234	2	.	.	.	5	8	.	3	.	.	.	2	1	.	.	.	.	145	63	10	843
47.022	169	29	26	.	1	5	3	.	.	.	.	.	.	.	.	.	.	3	.	17	2	10	265
47.025	83	58	5	.	3	1	4	3	.	.	4	1	.	.	.	.	.	1	.	10	1	2	176
47.028	264	118	40	.	16	.	14	15	2	9	5	.	.	.	.	.	1	1	.	52	15	10	562
47.032	208	141	72	.	4	2	15	10	2	8	5	.	1	.	1	.	1	7	.	22	2	8	509
47.034	139	36	8	.	3	1	7	27	.	3	5	.	.	.	1	.	.	2	.	45	7	18	302
47.035	223	73	23	.	16	2	20	43	.	11	7	1	.	.	.	.	.	4	.	29	1	10	463
47.040	205	85	29	.	5	2	8	24	.	4	34	.	.	.	.	.	1	3	.	127	18	22	567
47.049	64	109	20	.	1	8	26	50	.	6	.	2	.	.	.	.	1	11	.	12	2	35	347
47.053	265	102	9	.	2	8	27	27	.	12	.	.	1	.	.	.	.	17	.	82	7	21	580
47.057	300	116	5	.	.	13	50	29	.	11	.	1	.	.	1	.	2	33	.	114	6	50	731
47.061	79	20	9	1	.	4	11	17	.	7	22	.	.	.	.	3	.	12	.	33	4	9	231
47.065	99	93	7	.	.	11	30	5	.	4	8	54	.	.	.	.	.	8	.	22	5	19	365
47.069	140	51	64	.	.	8	143	10	.	5	.	.	.	1	1	3	.	1	.	38	6	9	480
47.070	90	18	13	.	.	11	188	8	.	.	.	.	.	.	.	1	.	5	.	34	2	.	370
47.074	138	14	19	.	1	8	301	5	.	.	.	.	.	.	.	.	.	2	.	65	11	23	587
47.078	11	5	5	.	.	.	64	2	.	.	.	.	.	.	.	.	.	.	.	9	.	6	102
47.082	119	6	13	.	.	.	80	7	.	.	.	.	.	.	.	.	.	.	.	29	1	2	257
47.086	248	11	59	.	.	.	530	.	3	2	.	.	.	.	.	.	.	.	.	127	2	20	1002
47.090	57	5	6	.	1	2	83	.	.	.	.	.	.	.	.	.	.	.	.	3	.	5	162
47.094	100	2	17	.	.	.	8	.	1	.	.	.	.	.	.	.	.	.	.	1	.	3	132
47.097	16	.	6	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	258	1	1	283
47.099	16	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	62	.	2	84
47.101	48	.	1	.	2	.	1	.	.	2	.	.	.	.	.	.	.	.	.	227	.	1	282
47.103	2	.	4	2	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	15
47.105	4	5	1	.	.	.	5	.	.	2	.	.	.	.	.	.	.	.	.	4	.	.	21
47.107	109	7	1	.	.	.	4	.	.	4	.	.	.	.	.	.	.	.	.	9	.	.	134
47.109	6	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	293	.	4	305
47.113	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	35	.	2	38
47.124	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	99	.	1	110
47.128	35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	96	6	.	137
47.132	85	9	1	7	.	.	3	.	3	4	.	.	.	.	.	.	.	.	.	46	.	.	158
47.134	21	9	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	52
47.137	17	12	4	.	.	.	3	.	2	5	1	.	.	.	.	1	.	.	.	1	.	2	48
47.139	16	11	.	2	.	.	5	.	.	4	.	.	.	.	.	.	.	.	.	9	.	.	47
47.141	24	17	.	4	.	.	13	.	2	3	.	.	.	.	.	.	.	.	.	18	.	9	90
47.143	23	2	1	26	4	.	16	.	.	1	.	.	.	.	.	.	.	.	.	4	3	9	89
47.145	15	14	1	4	1	.	5	.	3	3	1	.	.	.	.	3	.	.	.	.	.	2	52
47.147	44	78	3	18	2	1	16	.	.	.	3	.	.	.	2	4	.	.	.	5	1	4	181
47.149	40	28	3	7	.	4	15	.	.	3	1	.	.	.	.	6	.	.	.	3	1	8	119
47.151	22	3	.	.	.	.	4	.	.	1	2	.	.	.	.	1	.	.	.	6	.	11	50
47.153	30	13	.	.	.	1	17	.	5	5	1	.	.	.	.	9	.	.	.	6	8	5	100

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Myctophidae	Gonostomatidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Bathylagidae	Paralepididae	Scopelarchidae	Melamphaidae	Bregmacerotidae	Exocoetidae	Trachypteridae	Apogonidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
47.155	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
47.157	109	77	8	16	3	.	27	.	1	2	1	.	.	.	.	11	.	.	.	8	3	8	274
47.159	17	11	.	7	.	.	14	.	1	5	.	1	.	.	.	.	.	.	.	1	1	4	62
47.162	11	5	.	.	.	.	6	.	.	3	.	.	.	.	.	.	.	1	.	2	.	1	29
47.164	25	37	.	1	.	.	10	.	.	12	.	.	.	.	.	.	.	2	.	2	.	5	94
47.166	28	21	4	.	.	.	1	.	1	3	.	.	3	.	.	1	.	2	.	.	.	.	64
47.168	6	1	1	.	.	.	3	.	1	3	.	.	.	.	1	3	.	1	.	1	3	3	27
47.171	66	39	15	.	.	3	9	.	.	4	.	.	.	.	.	.	.	8	.	.	1	4	149
47.173	251	166	31	.	.	8	17	.	6	3	.	.	.	.	.	.	.	23	.	2	.	11	518
47.175	327	95	4	2	.	4	16	.	1	.	.	.	.	.	.	.	.	5	.	15	1	.	470
47.177	119	100	10	.	.	69	157	4	1	1	.	.	.	.	.	.	.	19	.	12	.	40	532
47.179	228	14	1	.	2	11	189	.	3	2	.	.	.	.	.	1	.	3	.	3	.	42	499
47.181	150	32	7	1	.	12	59	.	1	.	.	.	.	.	.	.	.	.	.	11	.	3	276
47.185	350	31	45	1	3	12	140	23	4	5	.	.	.	.	.	2	.	1	.	27	.	14	658
47.189	28	5	8	.	.	8	97	3	1	4	.	.	.	.	.	.	.	.	.	5	.	26	185
47.193	2	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
47.197	97	9	13	.	2	23	123	4	.	5	.	.	.	.	.	1	.	2	.	17	2	8	306
47.201	392	152	24	.	1	12	140	20	.	10	.	.	.	.	.	9	.	2	.	8	.	54	824
47.205	109	48	27	.	.	23	152	20	.	17	1	1	.	.	1	2	.	4	.	8	3	125	541
47.213	769	440	43	.	14	3	58	26	.	25	.	2	2	.	.	.	.	43	.	43	5	40	1513
47.217	440	90	44	.	6	4	30	20	.	4	.	1	.	.	.	.	.	5	.	20	.	11	677
47.221	452	36	54	.	13	2	30	43	.	9	.	.	.	.	.	2	1	3	.	17	.	14	676
47.225	512	151	53	.	5	7	34	31	5	6	2	.	2	1	1	.	4	15	.	16	2	13	860
47.229	496	272	83	.	14	5	17	11	1	9	2	.	1	.	.	1	1	5	.	21	.	3	942
47.233	1441	249	95	2	42	6	14	31	5	18	2	1	1	.	2	1	3	3	1	16	5	37	1975
47.237	100	17	18	.	4	.	8	2	1	3	.	.	.	.	.	.	1	1	.	7	.	3	165
47.240	201	46	51	.	5	.	3	3	.	1	.	2	.	.	2	1	3	16	.	13	.	1	348
47.242	953	94	18	.	2	2	20	3	.	6	9	.	.	.	.	2	.	8	1	14	.	6	1138
47.244	905	129	16	.	1	7	22	.	2	5	2	.	1	.	.	1	3	12	1	26	2	.	1135
47.246	111	8	6	.	.	1	2	.	.	1	.	.	.	.	.	.	1	12	.	4	.	2	148
47.250	297	18	.	.	.	6	3	.	.	.	1	.	.	.	.	.	.	5	.	15	3	1	349
47.254	245	27	11	.	1	2	8	1	.	3	2	.	.	.	.	1	.	8	.	15	2	.	326
47.258	516	38	6	.	.	.	3	.	.	.	9	.	.	.	.	.	1	6	1	109	37	26	752
47.268	55	15	1	.	.	.	1	.	.	6	72	.	1	.	1	.	1	.	6	29	3	.	191
47.272	21	6	5	.	.	.	.	.	.	2	.	.	.	.	.	.	1	11	1	18	12	9	86
47.276	1935	208	6	.	.	2	45	2	.	3	1	.	.	.	1	.	3	5	2	29	.	.	2242
47.278	54	38	.	.	.	.	6	.	.	.	.	.	1	.	1	.	.	1	2	8	.	.	111
47.280	175	8	3	.	.	2	14	.	.	5	.	.	.	.	.	.	.	1	.	1	.	.	209
47.283	184	6	6	.	.	.	4	.	.	2	.	.	.	.	.	.	.	3	.	5	.	2	212
47.286	1272	15	70	.	.	3	18	1	1	3	.	.	.	1	.	1	.	1	.	12	.	5	1403
47.288	1311	44	17	.	13	2	11	.	.	2	1	.	.	.	.	.	.	2	.	5	1	5	1414
47.290	186	11	93	.	2	3	4	.	.	10	2	.	.	.	2	.	1	.	.	2	.	3	319
47.292	276	30	46	.	6	.	7	4	.	9	2	.	.	.	2	.	.	5	.	9	3	3	402
47.295	702	101	103	1	4	6	7	15	.	8	1	1	1	2	1	.	1	4	2	17	4	4	985
47.297	552	136	64	.	4	16	17	11	.	16	3	1	2	5	.	.	4	13	.	26	1	11	882
47.301	438	54	71	.	5	8	8	10	2	15	2	1	.	.	1	.	3	6	.	8	2	.	634
47.304	92	21	27	.	1	1	4	7	.	9	2	.	2	.	.	.	1	2	.	6	2	3	180
47.306	309	68	70	.	5	18	15	10	2	12	1	.	1	1	1	1	3	13	.	18	4	18	570
47.310	780	154	54	.	9	33	18	51	2	8	10	.	.	2	5	3	2	36	.	42	22	18	1249
47.314	241	83	18	.	6	11	24	14	.	2	.	1	1	2	1	5	4	13	.	24	5	1	456
47.318	73	58	17	.	4	10	23	22	.	2	.	.	.	.	.	2	1	17	.	4	.	15	248
47.322	152	33	14	.	.	5	61	3	3	24	.	.	.	.	.	.	1	13	.	14	11	4	338

APPENDIX TABLE 1.—Counts of fish larvae, tabulated by family, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Myctophidae	Gonostomatidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Bathylagidae	Paralepididae	Scopelarchidae	Melamphaidae	Bregmacerotidae	Exocoetidae	Trachypteridae	Apogonidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other identified larvae	Unidentified larvae	Disintegrated larvae	Total fish larvae
47.326	217	40	11	.	.	2	152	15	1	58	.	.	2	.	1	4	.	26	.	50	.	3	582
47.330	436	148	80	.	2	11	137	56	1	14	.	.	.	.	.	12	.	16	.	18	1	15	947
47.334	165	29	32	.	1	9	53	21	.	3	.	.	.	.	.	2	.	4	.	1	.	1	321
47.338	78	19	51	.	.	8	24	8	.	4	.	.	.	.	.	.	.	7	.	.	.	.	199
47.342	302	24	62	3	1	2	19	32	1	8	.	.	.	.	.	4	.	4	.	10	.	.	472
47.345	856	45	78	2	2	11	26	6	.	11	.	.	.	.	.	.	.	15	.	.	.	9	1061
47.349	288	61	49	.	.	5	16	.	1	1	.	.	.	.	.	1	.	2	.	1	.	1	426
47.351	684	66	85	5	1	10	60	3	5	11	.	.	.	.	.	6	.	13	.	2	6	9	966
47.354	71	87	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	7	.	.	.	1	168
47.357	239	67	27	1	.	4	14	4	5	5	.	.	.	.	1	2	.	15	.	2	2	2	390
47.359	68	56	23	.	.	2	10	1	1	2	.	.	.	.	.	.	.	5	.	.	1	7	176
47.362	81	4	34	11	.	.	3	.	3	1	.	.	.	.	.	.	.	.	.	.	1	1	139
47.364	96	7	4	.	1	.	3	.	.	2	.	.	.	.	.	.	.	3	.	.	.	.	116
47.367	97	24	22	6	1	.	11	.	1	3	.	.	.	.	.	1	.	8	.	3	.	3	180
47.369	13	4	1	.	1	.	3	.	.	1	.	.	.	.	.	.	.	1	.	2	.	.	26
47.371	49	12	1	.	.	1	2	.	.	2	.	.	.	.	.	1	.	.	.	2	.	.	70
47.373	260	239	48	1	3	.	2	3	2	1	1	.	.	.	.	.	.	.	.	16	1	2	579
47.376	52	76	16	3	5	.	9	.	.	5	.	.	.	.	.	.	.	1	.	1	.	5	173
47.379	7	56	9	3	.	.	8	.	.	1	1	.	.	.	2	4	.	.	.	3	1	.	95
47.382	35	114	20	7	3	3	4	.	.	4	4	.	.	.	.	5	.	.	.	1	1	4	205
47.415	30	10	4	.	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	.	49
47.430	82	109	7	1	1	1	.	1	.	.	1	.	.	.	.	.	.	.	.	7	.	.	210
47.432	142	101	21	.	3	.	.	2	.	1	2	.	.	.	.	.	.	.	.	2	.	2	276
47.436	10	2	11	.	.	3	2	.	2	1	.	1	.	.	2	.	.	2	.	25	1	2	64
47.438	100	35	14	1	1	3	1	2	.	6	.	.	.	8	1	.	1	11	.	28	2	1	215
47.440	34	109	30	3	.	10	.	1	.	1	.	.	.	1	.	3	.	.	.	12	8	.	212
47.443	56	17	57	.	.	2	1	1	.	3	.	1	.	.	.	.	.	1	.	6	.	1	146
47.446	152	4	2	.	.	1	2	.	.	4	.	.	.	.	.	.	.	.	.	8	.	.	173
47.450	570	85	126	10		12	20	41	.	10	.	.	.	.	.	2	.	4	.	41	3	12	936
47.454	200	24	75	1	.	6	41	40	.	6	.	.	.	.	.	3	.	1	.	4	1	5	407
47.458	32	5	6	.	.	3	42	37	.	3	.	.	.	.	.	1	.	1	.	3	.	8	141
47.462	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
47.466	84	8	3	.	.	3	7	14	.	2	.	.	.	.	.	.	.	.	.	30	.	1	152
47.470	81	110	7	.	.	.	6	4	.	1	.	.	.	.	.	.	.	.	.	5	1	.	215
47.478	38	36	34	.	2	3	6	4	.	1	.	.	.	.	.	3	.	2	.	1	.	.	130
47.486	194	38	29	.	.	1	11	12	.	2	1	.	3	3	1	2	4	7	.	11	1	4	324
47.490	238	24	25	.	1	1	13	20	.	7	.	.	.	2	2	2	1	1	.	7	3	17	364
47.494	77	10	40	.	1	.	2	.	1	7	.	.	.	.	.	.	.	.	.	.	1	2	141
47.498	366	75	111	.	.	7	1	6	2	6	2	.	1	.	.	.	1	.	.	3	5	6	592
47.501	454	165	80	2	2	8	13	.	.	3	.	.	.	.	.	1	3	4	1	7	1	28	772
47.504	628	59	91	1	.	7	20	.	1	4	.	1	.	.	.	.	2	44	.	4	5	28	895
47.507	305	77	33	.	2	6	6	2	.	3	.	9	1	.	.	3	1	3	33	7	1	26	518
47.509	986	65	186	2	2	2	26	.	.	5	.	.	.	.	.	2	.	8	2	10	.	35	1331
47.511	346	2	4	.	2	.	11	.	.	1	.	1	.	.	.	.	.	1	.	3	1	.	372
47.513	80	4	.	.	.	.	.	.	.	3	.	2	1	.	.	.	.	2	.	2	.	.	94
47.515	35	11	14	.	.	.	7	.	.	3	.	.	.	.	.	.	.	2	.	1	1	6	80
47.517	34	36	1	.	.	.	1	.	.	3	.	.	.	.	.	.	.	3	2	4	.	1	85
47.520	55	80	.	.	4	.	3	3	1	6	.	.	.	.	.	.	.	4	.	44	.	1	201
47.523	4	30	.	.	1	.	7	.	1	3	.	.	.	.	.	.	.	3	5	8	.	1	63
47.525	7	10	.	.	.	.	6	.	1	2	3	.	.	.	.	.	1	.	4	13	1	4	52
47.527	550	132	.	.	2	.	3	.	.	3	753	.	.	.	.	.	1	5	25	580	52	12	2118

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on the second multi-vessel EASTROPAC survey (EASTROPAC II).

STATION NUMBER	Diogenichthys laternatus	Lampanyctus spp.	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lepidophanes pyrsobolus	Loweina laurae (rara)	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum spp. (other)	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Other identified[1] myctophids	Unidentified myctophids	Disintegrated myctophids	Total myctophids
45.016	2	5	.	1	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	12
45.018	9	10	.	1	.	1	10	1	.	2	.	.	.	.	.	.	.	.	.	.	.	1	35
45.020	10	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	1	1	.	.	.	.	14
45.021	7	1	.	.	.	.	4	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	13
45.023	13	6	.	.	5	.	35	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	61
45.024	20	6	.	.	4	2	52	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	86
45.026	27	1	.	.	3	1	4	1	.	2	.	.	.	.	1	.	.	.	.	.	.	.	40
45.028	22	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24
45.030	9	1	.	.	10	.	7	3	.	.	.	.	.	.	.	.	.	.	.	.	3	1	34
45.032	109	1	.	.	32	1	5	1	.	.	.	3	.	.	.	.	.	4	.	.	1	1	158
45.034	138	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	5	146
45.035	36	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	40
45.037	36	.	.	.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	41
45.039	52	.	.	.	12	1	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	4	77
45.041	22	1	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	29
45.043	14	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17
45.044	28	1	.	.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	50
45.046	23	1	.	.	16	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	43
45.048	20	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25
45.050	16	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	19
45.051	70	6	.	.	.	1	.	.	.	.	.	1	.	.	5	.	.	3	1	.	.	.	87
45.053	36	.	.	.	3	.	.	9	.	.	.	.	.	.	9	.	.	16	.	.	.	2	75
45.054	26	.	.	.	.	.	.	2	.	.	.	.	.	.	2	.	.	9	.	.	.	5	44
45.056	7	1	.	.	.	.	.	2	.	.	.	.	1	.	4	.	.	5	1	.	.	1	22
45.058	51	4	.	.	11	.	.	14	.	3	.	1	2	20	8	.	.	21	.	.	2	9	146
45.060	13	1	.	.	13	.	.	12	.	1	.	.	.	.	11	.	1	25	1	.	.	4	82
45.063	.	.	.	.	2	.	.	6	1	.	.	2	.	.	.	.	.	6	1	.	1	10	29
45.065	.	31	.	.	14	.	.	16	.	.	.	7	.	8	7	2	.	2	2	.	.	27	116
45.067	12	46	.	.	35	1	.	17	.	1	3	12	.	31	3	3	.	4	6	.	4	7	185
45.071	5	14	.	.	3	.	.	5	.	.	1	2	.	8	1	2	.	.	.	.	.	1	42
45.073	11	6	.	.	14	.	.	6	.	.	.	2	.	12	1	.	.	.	.	.	2	11	65
45.078	15	33	.	.	7	.	.	5	.	.	.	1	.	7	.	2	.	.	.	.	.	1	71
45.083	23	4	.	.	.	.	.	1	2	.	1	.	.	.	.	.	.	.	.	.	1	5	37
45.086	15	8	.	.	.	.	.	2	1	.	.	.	9	12	5	2	.	2	1	.	.	8	65
45.090	16	5	.	.	.	.	.	4	.	.	.	1	7	1	.	.	.	2	.	.	1	10	47
45.094	42	28	.	.	1	.	2	15	.	.	.	.	28	.	.	.	.	.	.	.	.	34	150
45.098	15	1	.	.	1	.	1	3	.	.	.	3	12	.	.	.	.	.	.	.	2	5	43
45.102	20	48	.	.	7	4	.	16	.	.	2	.	18	.	.	.	.	.	2	.	.	19	136
45.106	166	10	.	.	2	1	1	13	.	.	2	.	55	1	.	3	.	1	.	.	2	8	265
45.110	298	38	.	.	9	1	9	116	.	.	.	2	51	.	5	.	2	4	2	3	1	4	545
45.114	13	9	.	.	.	.	.	.	.	.	.	.	10	.	1	.	.	.	.	.	.	7	40
45.117	53	6	.	.	1	.	.	4	.	.	.	.	2	.	8	.	.	1	.	.	.	17	92
45.121	25	16	.	.	.	.	1	1	.	1	.	.	.	.	1	.	.	.	1	.	.	9	55
45.125	.	19	.	.	.	.	1	2	.	1	2	1	.	.	6	1	.	2	1	.	1	4	41
45.127	.	9	.	.	.	.	.	2	.	.	1	.	.	.	1	1	.	.	2	.	5	.	21
45.129	.	8	.	.	.	.	.	3	.	1	.	.	.	.	4	.	.	1	1	.	4	.	22
45.131	.	26	.	.	8	1	.	3	.	.	.	.	.	.	14	.	.	7	.	.	1	13	73
45.133	.	21	.	145	35	.	.	42	.	26	.	.	.	3	4	.	.	13	2	.	7	25	323
45.135	.	8	.	77	20	.	.	30	1	.	.	.	.	1	.	2	.	12	1	2	6	5	165
45.137	.	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	3	5	11
45.139	.	3	.	2	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	16	.	24
45.140	.	25	.	26	15	.	.	5	1	.	.	.	.	.	2	.	.	27	.	.	.	5	106

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on the second multi-vessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Diogenichthys laternatus	Lampanyctus spp.	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lepidophanes pyrosobolus	Loweina laurae (rara)	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum spp. (other)	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Other identified[1] myctophids	Unidentified myctophids	Disintegrated myctophids	Total myctophids
45.163	.	1	.	5	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	8
45.165	.	23	.	48	20	.	.	36	.	.	.	1	.	7	4	.	.	6	.	1	2	4	152
45.167	.	6	.	43	2	.	.	15	.	.	.	.	.	1	.	.	.	7	.	.	.	12	86
45.169	.	7	.	9	7	.	.	17	.	.	.	.	.	7	1	.	.	1	.	.	.	7	56
45.171	.	5	.	5	5	.	.	.	.	1	.	.	.	1	2	.	.	2	.	.	2	3	26
45.173	.	1	.	.	.	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
45.175	32	12	.	3	.	.	.	11	.	.	.	.	.	.	.	.	.	2	.	.	.	2	62
45.177	23	43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	70
45.179	39	12	.	.	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	5	59
45.183	14	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	26
45.187	244	8	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	255
45.191	115	13	.	.	.	.	1	2	.	.	.	.	1	.	2	.	2	.	3	.	.	5	144
45.194	27	3	.	.	.	.	.	3	.	.	.	.	4	.	.	.	.	.	2	.	.	10	49
45.198	116	35	.	.	1	.	10	3	.	.	.	.	44	.	1	.	1	.	1	.	.	39	251
45.202	10	24	.	.	1	.	.	.	.	.	.	.	16	.	.	1	.	.	.	.	.	1	53
45.206	4	10	.	.	.	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	4	22
45.283	26	56	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.	.	.	.	1	5	102
45.287	.	22	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	25
45.289	68	74	.	.	.	.	1	.	.	1	1	3	1	.	.	3	.	.	.	.	.	5	157
45.293	127	13	.	.	.	.	1	1	.	.	.	.	5	1	1	3	.	4	.	1	.	.	157
45.297	163	18	.	.	4	.	.	1	.	5	1	1	8	12	6	.	.	7	.	.	.	5	231
45.301	6	5	.	.	5	.	.	.	.	.	.	1	.	2	1	.	.	.	.	1	2	1	24
45.305	15	29	.	.	30	.	.	18	.	.	.	2	2	.	12	2	.	2	3	.	.	4	119
45.309	10	6	.	.	.	.	2	1	.	3	.	.	.	2	4	.	.	13	.	1	1	1	44
45.313	33	.	.	.	.	.	3	1	.	.	1	.	1	.	.	.	.	2	.	2	.	6	49
45.316	10	2	.	.	9	.	.	3	.	2	.	5	.	2	.	1	.	.	2	.	1	4	41
45.319	14	.	.	.	4	.	.	4	.	.	.	2	1	3	1	.	.	.	.	.	1	2	32
45.321	19	.	.	.	2	.	.	.	1	2	.	1	4	2	5	.	.	1	.	.	.	8	45
45.323	32	.	.	.	.	.	.	3	.	.	.	1	.	.	1	.	.	11	.	.	.	3	51
45.325	967	29	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	3	.	.	.	.	1002
45.329	49	16	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	69
45.331	218	13	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	235
45.333	84	12	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	108
45.335	47	.	.	.	16	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	65
45.337	37	1	.	.	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	49
45.339	9	.	.	.	15	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	26
45.341	17	2	.	.	26	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	47
45.343	6	.	.	.	9	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	17
45.344	3	1	.	.	15	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	21
45.346	6	2	.	.	10	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	19
45.348	12	5	.	.	9	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	30
45.350	39	1	.	.	25	.	3	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	70
45.352	17	.	.	.	4	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	29
45.356	40	.	.	.	24	.	1	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	69
45.358	46	.	.	.	49	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	98
45.360	9	1	.	.	5	.	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	18
45.362	1	.	5	.	26	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	36
45.365	.	.	58	.	39	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	99
45.367	5	.	.	.	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	5	23
45.369	53	2	9	.	34	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	101
45.371	32	1	.	.	50	.	28	.	.	.	.	5	.	.	.	.	.	.	.	.	1	3	120
45.373	59	1	.	.	36	.	20	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	117

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on the second multi-vessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Diogenichthys laternatus	Lampanyctus spp.	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lepidophanes pyrsobolus	Loweina laurae (rara)	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum spp. (other)	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Other identified[1] myctophids	Unidentified myctophids	Disintegrated myctophids	Total myctophids
45.375	20	.	.	.	8	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	1	2	34
45.377	42	.	.	.	22	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	67
45.379	42	8	.	.	63	.	85	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	199
45.381	59	.	.	.	13	.	19	.	.	.	.	5	.	.	.	.	.	.	.	.	.	2	98
45.383	37	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	40
45.385	7	.	.	.	1	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	19
45.387	6	12	.	.	2	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	1	2	26
CRUISE	46																						
46.002	.	.	.	.	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	14
46.004	7	1	.	.	94	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	103
46.006	2	.	.	.	27	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	30
46.007	1	.	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
46.009	.	1	.	.	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17
46.011	26	.	.	.	33	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	60
46.013	31	2	.	.	55	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	89
46.015	1	.	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18
46.017	1	.	.	.	23	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25
46.019	114	4	.	.	163	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	1	285
46.020	75	3	.	.	76	.	.	.	.	.	.	2	.	.	.	.	.	3	.	.	.	1	160
46.022	38	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	38
46.024	60	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	64
46.026	150	53	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	206
46.028	343	32	.	.	30	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3	412
46.030	80	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	3	85
46.032	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	1	1	9
46.034	117	8	.	.	6	1	.	.	.	.	.	.	2	.	11	.	.	5	.	.	1	1	152
46.036	357	20	.	.	.	.	.	.	.	.	.	3	2	.	36	.	.	14	1	.	.	3	436
46.038	12	1	.	.	.	.	.	.	.	.	.	.	1	.	3	.	.	1	.	.	1	1	20
46.040	19	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	2	.	25
46.042	31	1	.	.	2	.	.	3	2	8	.	4	.	1	2	.	1	4	2	.	1	.	62
46.044	69	3	.	.	6	.	.	.	.	.	.	.	.	.	3	.	.	4	.	.	.	4	89
46.046	51	1	.	.	16	.	.	.	3	1	.	2	.	1	.	.	.	.	.	.	.	3	78
46.048	50	1	.	.	5	.	.	1	.	.	1	.	.	3	.	.	.	1	1	.	.	.	63
46.050	163	13	.	.	8	.	.	14	1	2	.	4	4	12	8	.	1	9	2	1	.	8	250
46.052	207	21	.	.	5	.	2	9	.	10	1	3	2	23	13	2	1	9	.	.	11	.	319
46.054	126	23	.	.	.	.	.	1	.	.	.	3	5	11	16	1	.	15	.	.	.	10	211
46.055	65	15	.	.	.	2	1	.	.	.	2	.	4	1	6	.	.	1	.	.	.	3	100
46.057	366	241	.	.	4	11	3	17	.	17	2	8	31	.	5	13	.	8	22	.	3	.	751
46.059	133	250	.	.	.	9	11	.	.	8	.	5	10	3	6	16	.	3	17	.	3	20	494
46.061	71	36	.	.	.	1	.	.	.	.	.	.	11	.	1	2	.	.	1	.	.	25	148
46.063	14	27	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	3	48
46.065	189	84	.	.	7	5	18	14	.	.	1	.	56	.	.	24	.	1	3	.	.	2	404
46.067	164	73	.	.	3	.	7	4	.	.	.	.	7	.	.	3	1	.	1	.	3	3	269
46.069	46	64	.	.	2	.	.	1	.	.	.	1	2	.	.	.	.	.	.	.	.	.	116
46.071	21	34	.	.	2	.	.	.	.	.	2	.	1	.	.	1	.	.	.	.	1	10	72
46.075	19	14	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	35
46.077	30	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	36
46.079	285	28	.	.	4	21	.	.	.	.	.	2	18	.	.	33	.	1	13	.	1	2	408
46.082	35	2	.	.	1	6	.	.	.	.	.	1	4	.	.	5	.	.	.	.	5	2	61

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Diogenichthys laternatus	Lampanyctus spp.	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lepidophanes pyr-sobolus	Loweina laurae (rara)	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum spp. (other)	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Other identified[1] mycotophids	Unidentified myctophids	Disintegrated myctophids	Total myctophids
46.084	23	9	.	.	.	.	.	.	.	.	.	1	3	.	.	5	.	.	.	.	4	.	45
46.086	68	20	.	.	.	3	.	.	.	1	.	2	2	.	.	4	.	.	1	.	.	1	102
46.088	69	23	.	.	.	2	.	.	.	.	.	6	3	.	.	16	.	2	.	.	.	3	124
46.090	72	10	.	.	5	1	.	.	.	.	1	.	2	.	.	1	.	.	.	.	.	7	99
46.092	88	4	.	.	1	.	.	.	.	1	.	.	1	.	.	2	.	.	2	.	1	.	100
46.094	196	25	.	.	8	1	.	.	.	3	.	5	13	3	25	3	1	1	9	1	4	2	300
46.096	144	37	.	.	9	.	.	4	.	8	.	8	4	7	6	1	.	3	8	.	1	.	240
46.098	50	.	.	.	1	.	.	3	.	.	.	1	3	5	3	1	.	3	1	.	.	2	73
46.100	105	.	.	.	3	.	.	.	.	.	.	.	.	5	4	6	.	.	2	.	.	.	125
46.102	273	27	.	.	.	3	.	1	.	.	.	3	1	.	10	.	5	7	.	.	1	3	334
46.104	70	15	.	.	.	.	.	.	.	.	.	2	2	.	15	.	.	1	.	.	1	3	109
46.106	110	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	115
46.108	241	8	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	250
46.110	151	10	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	162
46.112	530	13	.	.	16	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1	.	562
46.114	12	.	.	.	16	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	31
46.116	9	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14
46.118	50	6	.	.	111	1	1	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	176
46.120	19	.	.	.	56	.	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	80
46.122	.	.	.	.	11	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3	2	17
46.124	.	.	.	.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
46.126	11	4	.	.	46	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	63
46.128	1	1	.	.	97	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	6	2	113
46.130	9	.	.	.	37	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	46
46.132	3	1	.	.	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26
46.134	2	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
46.135	.	.	81	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	81
46.137	201	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	201
46.139	160	14	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	175
46.141	435	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	438
46.143	112	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	113
46.145	269	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	282
46.147	480	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	484
46.149	1328	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1333
46.151	1358	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1358
46.153	2505	49	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	3	2561
46.155	939	20	.	.	1	5	.	.	.	.	.	3	.	.	1	.	.	4	.	.	.	.	973
46.157	474	3	.	.	.	2	.	.	.	.	.	3	1	.	4	.	.	1	.	.	1	1	490
46.159	59	1	.	.	4	2	.	.	.	.	.	.	1	.	1	.	1	.	1	.	1	.	71
46.161	268	17	.	.	.	3	.	1	.	.	2	3	2	.	39	2	.	3	6	1	3	.	350
46.163	214	28	.	.	1	4	.	1	.	3	.	3	2	.	12	.	5	7	4	.	1	5	290
46.165	48	7	.	.	.	.	.	1	.	11	1	5	4	.	6	1	.	4	.	.	1	1	90
46.167	131	25	.	.	.	.	.	.	.	.	.	23	5	.	3	3	.	2	.	.	1	2	195
46.169	89	34	.	.	2	2	.	.	.	.	1	.	3	.	3	13	1	6	1	.	4	4	163
46.171	182	8	.	.	1	1	.	.	.	.	.	.	30	.	.	14	.	3	5	.	.	11	255
46.173	27	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	33
46.175	44	4	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	2	52
46.177	105	8	.	.	1	.	.	.	.	.	.	.	1	.	.	4	.	.	5	.	.	.	124
46.179	182	14	.	.	1	.	.	.	.	.	.	.	1	.	.	6	1	1	3	.	.	4	213
46.181	20	5	.	.	1	1	.	.	.	.	.	.	5	.	.	.	.	1	2	.	17	.	52
46.183	50	9	.	.	4	1	1	.	.	.	.	.	9	.	.	4	.	1	6	.	.	.	85
46.185	178	36	.	.	8	2	.	.	.	.	.	2	8	.	.	11	.	4	11	.	1	1	262

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on the second multi-vessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Diogenichthys laternatus	Lampanyctus spp.	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lepidophanes pyrsobolus	Loweina laurae (rara)	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum spp. (other)	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Other identified[1] myctophids	Unidentified myctophids	Disintegrated myctophids	Total myctophids
46.187	468	40	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	2	2	.	.	1	516
46.189	234	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	236
CRUISE	47																						
47.001	68	13	.	.	8	2	.	.	.	.	.	2	1	.	.	1	.	1	1	.	.	.	97
47.005	161	33	9	.	33	1	.	.	.	.	.	19	6	.	.	.	.	17	1	.	.	7	287
47.008	205	31	5	.	4	2	.	.	.	.	.	4	.	.	.	.	.	3	1	.	.	2	257
47.011	117	22	13	.	2	.	.	.	.	.	.	3	.	.	.	.	.	3	1	.	.	.	161
47.019	287	37	2	.	39	.	.	.	.	.	.	1	.	.	.	.	.	2	2	.	.	.	370
47.022	148	11	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	2	.	5	.	169
47.025	73	5	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	2	83
47.028	175	66	.	.	5	1	.	.	.	.	.	7	.	.	.	.	.	9	.	.	1	.	264
47.032	148	38	.	.	12	.	.	.	.	.	.	3	.	.	.	.	.	6	1	.	.	.	208
47.034	95	23	.	.	.	1	.	.	.	.	.	7	4	.	.	.	.	6	.	.	.	3	139
47.035	171	21	.	.	1	3	.	.	.	.	.	9	12	.	.	.	.	3	1	.	1	1	223
47.040	129	38	11	.	3	.	.	.	.	.	.	10	6	.	.	.	.	.	.	.	6	2	205
47.049	42	9	.	.	1	.	.	.	.	.	.	4	3	.	.	.	.	1	2	.	1	1	64
47.053	105	89	.	.	1	4	.	.	.	.	.	19	18	.	.	11	.	2	3	.	9	4	265
47.057	192	50	.	.	.	1	.	.	.	.	.	23	1	.	.	6	.	1	12	.	11	3	300
47.061	22	12	.	.	3	2	.	.	.	.	.	4	23	.	.	1	.	.	9	.	.	3	79
47.065	31	22	.	.	1	3	.	.	.	.	.	2	12	.	.	.	.	.	22	.	.	6	99
47.069	29	6	.	.	2	3	.	.	.	.	.	.	35	.	.	28	.	2	5	.	30	.	140
47.070	50	11	.	.	.	.	.	.	.	.	.	1	17	.	.	.	.	1	10	.	.	.	90
47.074	98	4	.	.	1	1	.	.	.	.	.	.	26	.	.	1	.	.	5	.	2	.	138
47.078	5	.	.	.	1	.	.	.	.	.	.	.	3	.	.	.	.	.	2	.	.	.	11
47.082	70	10	.	.	.	.	.	.	.	.	.	.	11	.	.	.	.	.	6	.	15	7	119
47.086	212	10	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.	18	.	1	1	248
47.090	33	17	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	2	.	.	3	57
47.094	96	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	1	100
47.097	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	6	16
47.099	6	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	16
47.101	39	6	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	48
47.103	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2
47.105	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
47.107	30	70	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	6	.	.	1	109
47.109	1	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	6
47.113	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
47.124	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	10
47.128	.	31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	35
47.132	15	53	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	12	.	.	3	85
47.134	5	10	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	1	.	1	1	21
47.137	4	4	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	2	3	1	1	17
47.139	3	7	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	3	1	.	.	.	16
47.141	12	5	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	1	1	.	1	1	24
47.143	19	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	23
47.145	.	2	.	.	.	.	6	.	.	.	.	1	.	.	.	2	.	1	1	.	2	.	15
47.147	2	2	.	.	.	.	16	.	.	.	1	4	.	.	.	1	.	3	8	5	1	1	44
47.149	12	7	.	.	.	.	10	.	.	.	.	.	1	.	.	.	.	.	6	.	3	1	40
47.151	6	1	.	.	.	.	5	3	.	.	.	1	.	.	.	.	.	1	4	.	.	1	22
47.153	6	3	.	.	.	1	11	.	.	.	.	1	.	.	.	.	.	1	3	.	3	1	30

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on the second multivessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Diogenichthys laternatus	Lampanyctus spp.	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lepidophanes pyrsobolus	Loweina laurae (rara)	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum spp. (other)	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Other identified[1] myctophids	Unidentified myctophids	Disintegrated myctophids	Total myctophids
47.155	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
47.157	72	8	.	.	.	.	16	.	.	.	.	.	1	.	1	.	.	2	6	.	3	.	109
47.159	9	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	1	17
47.162	.	2	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	11
47.164	9	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	4	.	25
47.166	11	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	7	.	6	.	28
47.168	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	6
47.171	50	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	.	.	.	66
47.173	179	35	.	.	.	.	.	.	.	.	.	2	4	.	.	.	.	.	30	.	1	.	251
47.175	265	15	.	.	.	.	.	.	.	.	.	.	9	.	.	.	.	1	37	.	.	.	327
47.177	60	13	.	.	.	.	.	.	.	.	.	1	13	.	.	.	.	1	27	.	.	4	119
47.179	190	4	.	.	.	1	.	.	.	.	.	.	4	.	.	.	.	.	21	.	.	8	228
47.181	126	6	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	1	12	.	1	2	150
47.185	281	16	.	.	.	2	.	.	.	.	.	.	13	.	.	3	.	1	34	.	.	.	350
47.189	20	.	.	.	.	2	.	.	.	.	.	.	2	.	.	.	.	.	4	.	.	.	28
47.193	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
47.197	56	.	.	.	.	2	.	.	.	.	.	.	28	.	.	.	.	.	10	.	.	1	97
47.201	148	75	.	.	11	1	.	.	.	.	.	.	89	.	.	4	.	8	38	.	2	16	392
47.205	51	28	.	.	1	1	.	.	.	.	.	.	19	.	.	.	.	.	3	.	.	6	109
47.213	595	121	.	.	5	2	.	.	.	.	.	14	6	.	.	4	1	.	9	.	.	12	769
47.217	360	36	.	.	3	3	.	.	.	.	.	19	4	.	.	5	.	.	6	.	1	3	440
47.221	425	6	.	.	.	.	.	.	.	.	.	5	6	.	2	.	.	.	3	.	.	5	452
47.225	416	54	.	.	2	5	.	.	.	2	.	15	8	.	1	.	.	3	6	.	.	.	512
47.229	265	145	.	.	3	6	.	.	.	.	.	30	10	.	4	.	.	20	4	.	6	3	496
47.233	1206	146	.	.	12	6	.	.	.	.	.	23	.	.	3	1	.	33	2	.	2	7	1441
47.237	86	5	.	.	2	2	.	.	.	.	.	5	.	.	.	.	.	.	.	.	.	.	100
47.240	182	8	.	.	4	2	.	.	.	.	.	4	.	.	1	.	.	.	.	.	.	.	201
47.242	931	16	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	953
47.244	837	58	.	.	2	2	.	.	.	.	.	3	.	.	.	.	.	2	.	.	1	.	905
47.246	103	6	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	111
47.250	295	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	297
47.254	224	3	.	.	17	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	245
47.258	11	19	402	.	67	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	12	3	516
47.268	55	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	55
47.272	21	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21
47.276	1904	17	.	.	13	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1935
47.278	45	8	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	54
47.280	170	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	175
47.283	177	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	184
47.286	1260	10	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1272
47.288	1297	10	.	.	.	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	1311
47.290	172	6	.	.	.	.	.	.	.	.	1	4	.	.	.	.	.	2	.	.	.	1	186
47.292	266	4	.	.	.	.	.	.	.	.	.	3	.	.	1	.	.	.	1	.	.	1	276
47.295	627	28	.	.	.	2	.	.	.	.	.	8	1	.	13	.	.	16	.	1	2	4	702
47.297	432	51	.	.	.	2	.	.	.	.	.	12	4	.	17	.	.	27	2	.	.	5	552
47.301	382	25	.	.	.	8	.	.	.	.	.	7	.	.	6	.	.	10	.	.	.	.	438
47.304	56	16	.	.	.	.	.	.	.	.	.	4	2	.	4	.	1	7	1	.	.	1	92
47.306	241	16	.	.	.	3	.	.	.	.	.	19	5	.	11	.	.	13	.	.	.	1	309
47.310	552	116	.	.	.	5	.	.	.	1	.	44	3	.	11	.	.	19	4	.	16	9	780
47.314	145	62	.	.	.	.	.	.	.	1	.	18	2	.	1	4	.	.	3	.	5	.	241
47.318	49	8	.	.	.	.	.	.	.	.	.	4	6	.	.	.	.	2	1	.	.	3	73
47.322	111	11	.	.	2	1	.	.	.	.	.	2	19	.	.	2	.	.	3	.	1	.	152

APPENDIX TABLE 2.—Myctophid larvae, tabulated by genus or species, for all stations occupied on the second multi-vessel EASTROPAC survey (EASTROPAC II).—*Continued.*

STATION NUMBER	Diogenichthys laternatus	Lampanyctus spp.	Benthosema panamense	Ceratoscopelus townsendi	Diaphus spp.	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lepidophanes pyrsobolus	Loweina laurae (rara)	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum spp. (other)	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Other Identified myctophids	Unidentified myctophids	Disintegrated myctophids	Total myctophids
47.326	60	42	.	.	16	3	3	.	.	.	1	2	52	.	.	5	.	.	20	.	11	2	217
47.330	193	53	.	.	13	20	.	.	.	.	.	.	72	.	.	30	.	2	51	.	2	.	436
47.334	92	10	.	.	6	2	.	.	.	.	.	1	19	.	.	13	.	4	16	.	1	1	165
47.338	42	15	.	.	.	1	.	.	.	.	.	1	2	.	.	.	.	.	16	.	.	1	78
47.342	227	8	.	.	.	2	.	.	.	.	.	2	57	.	.	1	.	.	5	.	.	.	302
47.345	813	15	.	.	.	1	.	.	.	.	.	1	12	.	.	2	.	1	8	.	.	3	856
47.349	271	2	.	.	1	2	.	.	.	.	.	2	5	.	.	.	.	2	3	.	.	.	288
47.351	662	7	.	.	1	5	.	.	.	.	.	.	5	.	.	.	.	4	.	.	.	.	684
47.354	1	66	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	2	71
47.357	179	21	.	.	.	8	.	.	.	.	.	12	1	.	.	.	.	14	3	.	.	1	239
47.359	60	3	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	68
47.362	69	2	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	1	2	81
47.364	76	7	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	7	.	2	2	96
47.367	71	12	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	7	.	4	1	97
47.369	11	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	13
47.371	31	4	.	.	.	.	4	.	.	.	.	.	.	.	1	1	.	.	5	3	.	.	49
47.373	155	15	.	.	3	.	44	23	.	.	.	1	.	.	1	2	.	7	2	1	.	6	260
47.376	32	3	.	.	.	.	3	.	.	.	.	1	1	.	4	.	.	3	4	.	.	1	52
47.379	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	7
47.382	5	2	.	.	.	.	4	.	.	.	.	.	4	.	5	.	.	6	1	.	7	1	35
47.415	6	4	.	.	5	.	.	1	.	.	.	.	.	.	2	1	.	7	.	.	4	.	30
47.430	3	23	.	.	.	.	1	6	.	.	.	.	.	.	4	2	.	35	.	.	8	.	82
47.432	.	34	.	24	12	.	7	14	.	2	.	.	.	.	1	1	1	29	.	5	10	2	142
47.436	5	1	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	1	10
47.438	31	49	.	.	.	1	.	.	.	.	.	4	.	.	.	.	.	14	.	.	.	1	100
47.440	10	9	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	10	.	.	2	1	34
47.443	54	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	56
47.446	139	1	.	.	.	4	.	.	.	.	.	4	.	.	.	.	.	2	2	.	.	.	152
47.450	500	19	.	.	.	6	.	.	.	.	.	5	3	.	.	1	.	17	11	.	2	6	570
47.454	153	25	.	.	1	2	.	.	.	.	.	2	1	.	.	2	.	4	9	.	.	1	200
47.458	10	7	.	.	3	1	.	.	.	.	.	1	.	.	.	3	.	.	5	.	.	2	32
47.462	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
47.466	60	5	.	.	2	1	.	.	.	.	.	.	4	.	1	6	.	1	4	.	.	.	84
47.470	39	16	.	.	3	.	.	.	.	.	.	.	14	.	.	2	.	.	6	.	1	.	81
47.478	19	10	.	.	.	.	.	1	.	.	.	4	.	.	1	1	.	.	1	.	1	.	38
47.486	150	12	.	.	.	1	.	1	.	1	2	1	1	.	9	2	.	2	3	.	.	9	194
47.490	199	.	.	.	.	2	.	.	.	2	.	5	2	.	5	5	.	.	6	.	.	12	238
47.494	63	4	.	.	.	.	.	.	.	.	.	1	.	.	3	.	1	.	1	.	.	4	77
47.498	296	16	.	.	1	2	.	.	.	2	.	2	4	.	13	1	8	12	2	.	.	7	366
47.501	401	33	.	.	.	3	.	.	.	.	.	5	2	.	.	.	1	3	.	.	.	6	454
47.504	568	15	.	.	.	1	1	.	.	.	3	6	.	.	9	.	1	3	.	.	.	21	628
47.507	272	23	.	.	.	4	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	3	305
47.509	955	24	.	.	.	3	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	2	986
47.511	344	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	346
47.513	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	80
47.515	34	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	35
47.517	32	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	34
47.520	26	9	.	.	18	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	55
47.523	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
47.525	1	1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
47.527	.	.	524	.	24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	550

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC II.

STATION NUMBER	Vinciguerria spp.	Cyclothone spp.	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia sp.	Diplophos taenia	Ichthyococcus irregularis	Maurolicus muelleri	Astronesthidae	Bathophilus filifer	Stomias sp.	Evermannellidae	Macroparalepis macrurus	Scopelosauridae	Scomberesocidae	Gempylus serpens	Nealotus tripes	Diplospinus multistriatus	Trichiurus lepturus	Tetragonurus spp.	Trachichthyidae	Balistidae	Ostraciontidae	Total; selected categories
45.016	12	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14
45.018	77	3	.	.	.	2	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	87
45.020	5	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	7
45.021	15	1	.	.	.	1	.	.	.	4	1	.	1	.	.	2	.	.	.	.	.	.	.	25
45.023	101	5	.	.	.	.	.	.	.	2	1	1	.	.	.	.	.	.	.	.	.	.	.	110
45.024	95	1	.	.	.	.	.	.	.	.	1	.	.	.	.	2	.	1	.	.	.	.	.	100
45.026	27	.	4	.	.	3	.	.	.	.	.	.	1	.	.	1	.	1	.	.	.	.	1	38
45.028	21	.	9	.	.	1	.	.	.	3	1	.	.	.	.	1	.	.	.	.	.	.	.	36
45.030	54	1	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	61
45.032	108	.	7	.	.	3	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	10	129
45.034	35	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	39
45.035	27	.	2	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	34
45.037	24	.	10	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	35
45.039	77	3	1	.	.	2	.	.	.	2	.	.	1	.	.	1	3	.	.	.	.	.	.	90
45.041	49	.	8	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	58
45.043	16	.	5	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	23
45.044	38	1	4	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	45
45.046	56	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	59
45.048	21	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	23
45.050	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
45.051	8	5	4	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
45.053	7	12	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	22
45.054	2	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
45.056	4	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	8
45.058	11	4	1	.	.	3	.	.	.	.	.	3	1	.	.	1	.	.	.	.	.	.	.	24
45.060	1	3	1	.	.	.	.	.	3	2	.	.	.	.	.	2	.	.	.	.	.	.	.	12
45.063	43	7	1	.	.	1	.	.	.	7	.	2	1	.	.	1	.	.	.	.	.	.	.	58
45.065	352	5	.	.	.	1	.	.	.	12	4	4	3	.	.	.	.	.	.	.	.	.	.	397
45.067	560	23	3	.	.	1	.	.	1	39	6	24	28	.	.	.	.	.	.	.	.	.	.	685
45.071	39	1	.	.	.	.	.	.	.	1	1	4	1	.	.	.	.	.	.	.	.	.	.	47
45.073	65	3	2	.	.	.	.	.	.	.	.	1	1	.	.	.	1	.	.	.	.	.	.	73
45.078	105	1	1	.	.	1	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	110
45.083	26	.	.	.	1	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	30
45.086	77	.	3	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	81
45.090	65	2	6	.	.	.	.	.	.	3	.	5	.	.	.	.	.	.	.	1	.	.	.	84
45.094	100	7	8	.	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	116
45.098	15	.	2	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	18
45.102	78	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	86
45.106	21	.	5	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	28
45.110	27	5	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	47
45.114	15	3	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	22
45.117	43	5	1	.	.	.	1	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	52
45.121	91	7	4	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	104
45.125	291	24	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	327
45.127	38	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	41
45.129	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
45.131	325	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	339
45.133	3	33	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	36
45.135	6	10	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	18
45.137	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
45.139	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
45.140	12	38	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	52

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC II.—*Continued.*

STATION NUMBER	Vinciguerria spp.	Cyclothone spp.	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia sp.	Diplophos taenia	Ichthyococcus irregularis	Maurolicus muelleri	Astronesthidae	Bathophilus filifer	Stomias sp.	Evermannellidae	Macroparalepis macrurus	Scopelosauridae	Scomberesocidae	Gempylus serpens	Nealotus tripes	Diplospinus multistriatus	Trichiurus lepturus	Tetragonurus spp.	Trachichthyidae	Balistidae	Ostraciontidae	Total: selected categories
45.163	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
45.165	33	29	.	.	.	2	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	66
45.167	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
45.169	5	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
45.171	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
45.173	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
45.175	20	7	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	28
45.177	141	7	.	.	1	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	151
45.179	32	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33
45.183	13	1	4	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	20
45.187	15	1	16	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33
45.191	10	.	3	.	1	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20
45.194	4	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
45.198	16	3	7	.	2	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	32
45.202	15	4	2	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24
45.206	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
45.283	8	.	2	.	2	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17
45.287	79	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	84
45.289	114	10	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	127
45.293	55	2	4	.	.	.	.	1	.	4	.	.	.	.	.	.	1	.	.	.	.	.	.	67
45.297	103	3	7	.	.	1	.	.	.	15	.	.	.	.	.	.	.	.	.	.	.	.	.	129
45.301	24	1	8	.	1	1	.	.	.	3	.	3	.	.	.	.	.	.	.	.	.	.	.	41
45.305	1035	5	2	.	1	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	1046
45.309	148	1	.	.	1	1	.	.	3	4	.	.	.	.	.	.	.	.	.	.	.	.	.	158
45.313	34	.	2	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	38
45.316	31	3	1	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	38
45.319	45	1	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	48
45.321	9	3	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
45.323	2	2	1	.	.	.	.	.	2	1	.	.	.	.	.	1	.	.	.	.	.	.	.	9
45.325	17	11	42	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	72
45.329	2	3	3	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	8
45.331	2	3	13	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	20
45.333	27	1	5	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	13	47
45.335	27	2	8	.	.	3	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	8	51
45.337	12	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	14
45.339	5	.	2	.	.	3	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	5	18
45.341	69	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	74
45.343	32	.	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	36
45.344	34	.	1	.	.	3	.	.	.	2	.	.	1	.	.	2	.	.	.	.	.	.	2	45
45.346	19	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	21
45.348	120	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	1	123
45.350	296	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	298
45.352	65	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	69
45.356	147	.	11	.	.	6	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	165
45.358	102	.	1	.	.	5	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	109
45.360	32	.	7	.	.	5	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	45
45.362	27	.	6	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37
45.365	55	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	56
45.367	16	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17
45.369	103	.	3	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	108
45.371	232	.	13	.	.	9	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	253
45.373	146	.	14	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	164

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC II.—*Continued.*

STATION NUMBER	Vinciguerria spp.	Cyclothone spp.	Bathylagus nigrigenys	Leuroglossus stilbius urotramus	Nansenia sp.	Diplophos taenia	Ichthyococcus irregularis	Maurolicus muelleri	Astronesthidae	Bathophilus filifer	Stomias sp.	Evermannellidae	Macroparalepis macrurus	Scopelosauridae	Scomberesocidae	Gempylus serpens	Nealotus tripes	Diplospinus multistriatus	Trichiurus lepturus	Tetragonurus spp.	Trachichthyidae	Balistidae	Ostraciontidae	Total: selected categories
45.375	39	.	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	43
45.377	75	.	8	.	.	11	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	95
45.379	797	1	2	.	.	7	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	1	.	812
45.381	244	.	4	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	253
45.383	18	.	4	.	.	2	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	26
45.385	60	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	61
45.387	428	1	.	.	.	.	.	.	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	433
CRUISE	46																							
46.002	18	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21
46.004	118	.	4	.	.	4	.	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	130
46.006	18	.	1	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	21
46.007	28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	28
46.009	22	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24
46.011	69	.	1	.	.	3	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	75
46.013	47	.	.	.	.	4	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	1	57
46.015	16	.	1	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	19
46.017	4	.	5	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	11
46.019	147	.	1	.	.	1	.	.	.	2	.	.	.	.	.	2	1	.	.	.	.	.	.	154
46.020	78	.	10	.	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	92
46.022	14	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	16
46.024	21	6	5	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	33
46.026	131	9	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	145
46.028	154	2	12	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	171
46.030	7	.	8	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	16
46.032	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
46.034	35	5	5	.	.	.	.	.	1	.	.	.	.	.	.	3	.	.	.	.	.	.	.	49
46.036	91	36	7	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	136
46.038	4	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
46.040	19	1	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	23
46.042	129	4	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	137
46.044	95	.	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	98
46.046	56	1	1	.	1	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	61
46.048	53	1	10	.	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	67
46.050	175	6	12	.	.	.	1	1	.	.	.	1	3	.	.	2	.	.	.	.	.	.	.	201
46.052	206	5	7	.	.	.	.	2	.	.	.	8	2	.	.	.	1	.	.	.	.	.	.	235
46.054	177	2	20	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	202
46.055	66	4	5	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	78
46.057	610	36	10	.	.	.	.	.	.	1	.	2	1	2	.	1	.	.	.	.	.	.	.	665
46.059	480	23	2	.	.	.	.	.	.	1	2	.	.	14	.	.	3	.	.	1	.	.	.	526
46.061	85	7	3	.	3	.	.	6	1	.	.	.	.	10	.	.	.	.	.	1	.	.	.	116
46.063	16	.	2	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21
46.065	76	16	4	.	.	.	.	3	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	103
46.067	104	13	5	.	2	.	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	129
46.069	52	1	22	.	5	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	82
46.071	26	.	14	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	45
46.075	20	1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26
46.077	17	2	1	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	.	.	23
46.079	23	.	23	.	1	.	1	6	8	.	.	.	.	3	.	.	.	.	.	.	.	.	.	65
46.082	10	.	17	.	.	.	.	36	4	.	.	.	.	7	.	.	.	.	.	.	.	.	.	74

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC II.—*Continued.*

STATION NUMBER	Vinciguerria spp.	Cyclothone spp.	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia sp.	Diplophos taenia	Ichthyococcus irregularis	Maurolicus muelleri	Astronesthidae	Bathophilus filifer	Stomias sp.	Evermannellidae	Macroparalepis macrurus	Scopelosauridae	Scomberesocidae	Gempylus serpens	Nealotus tripes	Diplospinus multistriatus	Trichiurus lepturus	Tetragonurus spp.	Trachichthyidae	Balistidae	Ostraciontidae	Total: selected categories
46.084	17	1	21	.	6	.	2	19	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	67
46.086	66	2	33	.	2	.	1	169	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	274
46.088	27	7	8	.	1	.	2	24	.	1	.	.	.	1	.	.	1	.	.	.	.	.	.	72
46.090	17	4	4	.	.	.	.	3	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	29
46.092	13	5	3	.	.	.	.	11	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	36
46.094	145	9	3	.	.	.	2	.	1	.	.	2	1	.	.	.	.	.	.	.	.	.	.	163
46.096	226	21	13	.	.	.	2	.	.	.	.	3	3	.	.	.	2	.	.	.	.	.	.	270
46.098	40	2	2	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	52
46.100	6	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
46.102	48	6	3	.	1	.	2	.	.	4	.	.	3	.	.	.	.	.	.	.	.	.	.	67
46.104	46	2	.	.	.	.	.	.	.	1	.	.	1	.	.	1	.	.	.	.	.	.	.	51
46.106	34	7	9	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	52
46.108	36	2	27	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	69
46.110	10	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15
46.112	75	.	16	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	93
46.114	6	.	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	10
46.116	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
46.118	85	.	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	89
46.120	100	.	1	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	103
46.122	29	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33
46.124	22	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24
46.126	98	.	10	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	109
46.128	130	.	8	.	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	142
46.130	53	.	11	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	66
46.132	26	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	35
46.134	12	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20
46.135	12	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20
46.137	28	.	24	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	54
46.139	50	1	11	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	64
46.141	20	.	18	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	41
46.143	14	1	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	27
46.145	118	1	38	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	157
46.147	41	.	41	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	83
46.149	11	3	22	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	37
46.151	4	4	13	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	22
46.153	163	1	4	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	169
46.155	132	8	6	.	.	.	.	.	.	2	.	.	.	.	.	2	6	.	.	.	.	.	.	156
46.157	24	2	6	.	.	.	1	.	.	.	.	.	2	.	.	4	1	.	.	.	.	.	.	40
46.159	10	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	15
46.161	35	12	8	.	1	.	.	2	.	2	.	2	.	.	.	.	4	.	.	.	.	.	.	64
46.163	80	4	10	.	.	.	.	4	.	3	.	.	.	.	.	1	1	.	.	.	.	.	.	103
46.165	22	7	12	.	.	.	.	7	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	56
46.167	25	4	37	.	.	.	1	10	.	.	.	.	.	.	.	.	5	.	.	.	.	.	.	82
46.169	149	1	52	.	.	.	1	85	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	290
46.171	13	.	44	.	.	.	1	41	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.	103
46.173	1	.	9	1	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25
46.175	1	.	21	.	.	.	.	74	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	96
46.177	20	5	45	.	.	.	3	5	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	80
46.179	82	1	135	.	.	.	2	24	1	.	.	.	.	1	.	.	.	.	.	.	1	.	.	247
46.181	53	4	132	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	191
46.183	17	3	47	.	4	.	1	.	3	.	2	.	.	1	.	.	.	.	.	.	.	.	.	78
46.185	90	5	45	.	1	.	2	.	3	.	2	.	.	.	.	.	.	.	.	.	.	.	.	148

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC II.—*Continued.*

STATION NUMBER	Vinciguerria spp.	Cyclothone spp.	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia sp.	Diplophos taenia	Ichthyococcus irregularis	Maurolicus muelleri	Astronesthidae	Bathophilus filifer	Stomias sp.	Evermannellidae	Macroparalepis macrurus	Scopelosauridae	Scomberesocidae	Gempylus serpens	Nealotus tripes	Diplospinus multistriatus	Trichiurus lepturus	Tetragonurus spp.	Trachichthyidae	Balistidae	Ostraciontidae	Total: selected categories
46.187	39	3	17	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	60
46.189	5	.	8	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	15
CRUISE	47																							
47.001	61	2	4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	11	.	.	.	.	79
47.005	203	3	6	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	5	.	.	.	.	219
47.008	49	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	62
47.011	26	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30
47.019	221	13	5	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	18	.	.	.	.	258
47.022	27	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13	.	.	.	.	45
47.025	58	.	4	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	63
47.028	117	1	14	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	133
47.032	137	4	15	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	159
47.034	36	.	7	.	.	.	.	.	.	.	.	.	.	10	.	.	4	.	.	.	.	.	.	57
47.035	70	3	20	.	.	.	.	.	.	1	.	.	.	8	.	3	1	.	.	.	.	.	.	106
47.040	76	.	8	.	.	.	.	7	.	.	.	.	1	2	.	.	7	.	.	.	.	.	.	101
47.049	92	1	26	.	.	.	.	14	2	2	.	.	.	5	.	.	3	.	.	.	.	.	.	145
47.053	94	1	27	.	.	.	1	5	.	6	.	.	1	59	.	.	8	.	3	.	.	.	.	205
47.057	106	3	50	.	.	.	3	3	.	.	.	.	.	55	.	.	47	.	4	.	.	.	.	271
47.061	18	.	11	.	.	.	.	1	.	.	.	.	.	6	.	.	16	.	3	.	.	.	.	55
47.065	91	.	26	4	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	122
47.069	49	.	21	122	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	14	.	.	207
47.070	17	.	12	176	.	.	.	1	.	.	4	.	.	.	1	.	1	.	.	.	21	.	.	233
47.074	14	.	7	294	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	20	.	.	337
47.078	4	.	3	61	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	2	.	.	71
47.082	6	.	1	79	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	86
47.086	11	.	3	527	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	541
47.090	5	.	6	77	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	89
47.094	2	.	1	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	11
47.097	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
47.099	.	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3
47.101	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	3
47.103	.	.	2	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	3
47.105	5	.	5	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	11
47.107	7	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
47.109	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.113	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
47.124	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
47.128	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
47.132	8	1	3	.	.	.	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.	.	15
47.134	8	.	.	.	.	.	.	.	.	.	.	.	.	.	19	.	.	1	.	.	.	.	.	28
47.137	9	1	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	14
47.139	11	.	5	.	.	.	.	.	.	.	.	.	.	.	4	.	.	1	.	.	.	.	.	21
47.141	16	.	13	.	.	.	.	.	.	.	.	.	.	.	4	.	.	1	.	.	.	.	.	34
47.143	2	.	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	22
47.145	14	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
47.147	76	1	16	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	97
47.149	27	.	15	.	.	.	.	.	2	1	.	.	.	.	.	.	.	3	.	.	.	.	.	48
47.151	3	.	4	.	.	.	.	.	.	.	.	.	.	.	1	.	.	5	.	.	.	.	.	13
47.153	9	4	17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	.	.	35

APPENDIX TABLE 3.—Counts of selected categories of fish larvae tabulated by station, EASTROPAC II.—*Continued.*

STATION NUMBER	Vinciguerria spp.	Cyclothone spp.	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Nansenia sp.	Diplophos taenia	Ichthyococcus irregularis	Maurolicus muelleri	Astronesthidae	Bathophilus filifer	Stomias sp.	Evermannellidae	Macroparalepis macrurus	Scopelosauridae	Scomberesocidae	Gempylus serpens	Nealotus tripes	Diplospinus multistriatus	Trichiurus lepturus	Tetragonurus spp.	Trachichthyidae	Balistidae	Ostraciontidae	Total selected categories
47.155	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
47.157	74	3	27	.	.	.	.	.	.	.	.	.	.	.	.	.	1	7	.	.	.	.	.	112
47.159	11	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	26
47.162	5	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	12
47.164	37	.	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	49
47.166	19	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	22
47.168	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	5
47.171	38	1	9	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	50
47.173	165	1	17	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	189
47.175	95	.	15	1	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	114
47.177	100	.	34	123	.	.	.	.	.	.	69	.	.	.	1	.	.	.	.	.	.	.	.	327
47.179	14	.	28	161	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	1	.	.	207
47.181	31	.	15	44	.	.	.	1	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	97
47.185	30	1	21	119	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	177
47.189	4	.	27	70	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	1	.	.	104
47.193	2	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	4
47.197	7	.	31	92	.	.	1	.	.	.	.	.	.	2	1	.	.	.	.	.	1	.	.	135
47.201	142	4	66	74	.	.	.	.	2	.	.	.	.	2	.	.	.	.	.	.	2	.	.	292
47.205	38	1	125	27	.	.	.	6	.	1	1	.	.	7	.	.	1	.	.	.	.	.	.	207
47.213	415	12	58	.	.	.	2	7	.	1	.	.	.	36	.	1	2	.	.	.	.	.	.	534
47.217	84	1	30	.	.	.	1	3	.	.	.	.	1	13	.	.	2	.	.	.	.	.	.	135
47.221	30	1	30	.	.	.	5	.	.	.	.	.	1	13	.	1	2	.	.	.	.	.	.	83
47.225	146	4	34	.	.	.	.	.	2	.	.	.	.	2	.	3	6	.	.	.	.	.	.	197
47.229	256	16	17	.	.	.	.	.	1	2	.	.	1	.	.	1	4	.	.	.	.	.	.	298
47.233	241	6	14	.	.	.	.	.	1	.	.	.	2	.	.	2	6	.	.	.	.	.	.	274
47.237	16	1	8	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	26
47.240	44	2	3	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	50
47.242	91	3	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	115
47.244	124	5	22	.	.	.	.	.	.	5	.	.	.	.	.	1	2	.	7	.	.	.	.	166
47.246	7	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	11
47.250	13	.	3	.	.	.	.	.	.	3	3	.	.	.	.	1	1	.	7	.	.	.	.	36
47.254	27	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	39
47.258	36	1	3	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	5	.	.	.	.	47
47.268	15	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16
47.272	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	8
47.276	208	.	45	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	9	.	.	.	.	264
47.278	33	5	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	47
47.280	7	1	14	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	24
47.283	4	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
47.286	12	2	13	.	.	.	1	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	36
47.288	44	.	11	.	.	.	.	.	.	1	.	.	.	.	.	.	2	.	.	.	.	.	.	58
47.290	11	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	16
47.292	29	1	7	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.	.	.	44
47.295	91	9	7	.	.	.	1	.	.	5	.	.	.	.	.	8	4	.	.	.	.	.	.	125
47.297	122	14	17	.	.	.	.	.	1	9	3	.	.	3	.	13	6	.	.	.	.	.	.	187
47.301	53	1	8	.	.	.	.	.	1	5	.	.	1	.	.	6	1	.	.	.	.	.	.	76
47.304	17	4	4	.	.	.	.	.	.	1	.	.	.	.	.	1	1	.	.	.	.	.	.	28
47.306	60	5	15	.	.	.	.	.	1	6	1	.	.	.	.	8	1	.	.	.	.	.	.	100
47.310	142	11	18	.	.	.	.	.	4	22	.	.	2	.	.	10	10	.	.	.	.	.	.	219
47.314	75	4	24	.	.	.	.	4	2	5	.	1	1	12	.	1	4	.	.	.	.	.	.	133
47.318	45	.	23	.	.	.	.	13	.	2	.	.	.	4	.	.	.	.	.	.	.	.	.	87
47.322	22	1	59	2	.	.	2	5	.	2	.	.	.	8	.	.	.	.	.	.	.	.	.	101

APPENDIX TABLE 3.—Counts of selected categories of fish larvae, tabulated by station, EASTROPAC II.—*Continued.*

STATION NUMBER	Vinciguerria spp.	Cyclothone spp.	Bathylagus nigrigenys	Leurogloseus stilbius urotaenia	Nansenia sp.	Diplophos taenia	Ichthyococcus irregularis	Maurolicus muelleri	Astronesthidae	Bathophilus filifer	Stomias sp.	Evermannellidae	Macroparalepis macrurus	Scopelosauridae	Scomberesocidae	Gempylus serpens	Nealotus tripes	Diplospinus multistriatus	Trichiurus lepturus	Tetragonurus spp.	Trachichthyidae	Balistidae	Ostraciontidae	Total: selected categories
47.326	33	1	143	9	.	.	6	.	.	.	1	.	.	43	.	.	.	.	.	.	.	.	.	236
47.330	129	5	123	14	.	.	2	11	1	.	10	.	.	16	.	.	.	.	.	.	.	.	.	311
47.334	28	.	45	3	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	89
47.338	19	.	19	5	.	.	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	51
47.342	24	.	17	2	.	.	.	.	.	.	1	.	.	3	7	.	.	.	.	.	.	.	.	54
47.345	44	1	26	.	.	.	.	.	.	1	5	.	.	.	.	.	.	.	.	.	.	.	.	77
47.349	61	.	16	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	79
47.351	66	.	60	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	127
47.354	87	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	87
47.357	66	1	14	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	85
47.359	56	.	10	.	.	.	.	.	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	69
47.362	4	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
47.364	7	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
47.367	22	2	11	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	38
47.369	3	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	8
47.371	7	5	2	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2	.	.	.	.	.	17
47.373	237	2	2	.	.	.	.	.	.	.	.	.	2	.	.	.	.	16	.	.	.	.	.	259
47.376	72	3	9	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	85
47.379	55	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	66
47.382	103	1	4	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	111
47.415	7	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	11
47.430	108	1	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	1	.	.	.	.	.	114
47.432	69	32	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	103
47.436	2	.	2	.	.	.	.	.	.	1	.	.	.	.	22	.	1	1	.	.	.	.	.	29
47.438	34	1	1	.	.	.	.	.	.	2	.	.	.	.	15	.	8	3	.	.	.	.	.	64
47.440	107	2	.	.	.	.	.	.	.	10	.	.	.	.	7	.	3	.	.	.	.	.	.	129
47.443	17	.	1	.	.	.	.	.	.	2	.	.	.	.	6	.	.	.	.	.	.	.	.	26
47.446	4	.	2	.	.	.	.	.	.	1	.	.	.	.	7	.	.	.	.	.	.	.	.	14
47.450	76	9	20	.	.	.	.	.	.	5	.	.	.	.	37	.	2	.	.	.	.	.	.	149
47.454	21	3	41	.	1	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	68
47.458	5	.	42	.	.	.	.	.	1	.	2	.	.	1	.	.	.	.	.	1	.	.	.	52
47.462	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
47.466	6	.	7	.	1	.	.	2	.	.	.	.	.	26	.	.	.	.	.	.	.	.	.	42
47.470	3	.	6	.	.	.	.	107	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	119
47.478	26	1	6	.	.	.	.	9	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	45
47.486	30	2	11	.	.	.	.	5	.	.	.	.	.	.	.	2	3	.	.	.	.	.	.	53
47.490	14	.	13	.	.	.	3	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37
47.494	10	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
47.498	65	8	1	.	1	.	2	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	78
47.501	148	17	13	.	.	.	.	.	.	1	.	.	.	.	.	2	3	.	.	.	.	.	.	184
47.504	49	9	20	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	79
47.507	75	2	6	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	85
47.509	64	.	26	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	93
47.511	2	.	11	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13
47.513	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
47.515	9	2	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18
47.517	36	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37
47.520	80	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	83
47.523	30	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	37
47.525	10	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16
47.527	132	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	135

APPENDIX TABLE 4.—Summary of occurrences and numbers of larvae of 23 categories, limited in distribution to a broad coastal band or around offshore islands or banks.

STATION NUMBER	Engraulis ringens	Gobiidae	Albula vulpes	Etrumeus acuminatus	Opisthonema sp.	Sardinops sagax	Engraulidae (other)	Synodontidae	Bothus leopardinus	Citharichthys spp.	Cyclopsetta sp.	Syacium ovale	Symphurus spp.	Carangidae	Eucinostomus sp.	Labridae	Mugilidae	Polynemidae	Pomacentridae	Sciaenidae	Scorpaenidae	Serranidae	Carapidae	Total: 23 categories
45.339	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
45.343	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
45.350	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
45.358	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
45.360	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	1	.	.	.	.	1	.	.	4
45.362	.	d	.	.	.	.	1	.	.	.	.	2	.	1	.	1	.	2	.	.	.	1	.	16
45.365	.	31	.	.	.	.	11	1	1	.	.	2	4	11	.	.	.	19	.	.	10	.	.	90
45.367	.	5	.	.	.	.	2	.	1	.	.	.	.	2	.	.	.	.	.	.	.	3	.	13
45.369	.	20	.	.	.	.	1	.	.	.	.	4	1	10	.	2	.	.	6	.	.	9	.	53
45.371	.	1	.	.	.	.	.	.	.	.	.	4	.	.	.	2	.	.	.	.	.	.	.	7
45.373	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	5	.	.	.	.	1	.	.	8
45.375	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	2
45.377	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	5	.	.	11
45.379	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
45.381	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	2
CRUISE 46																								
46.002	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
46.004	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2
46.006	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
46.007	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
46.009	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2
46.011	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2
46.042	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
46.052	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	3
46.059	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
46.082	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
46.108	.	.	.	.	.	.	.	.	1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	3
46.110	.	.	.	.	.	.	.	.	4	.	.	8	.	.	.	.	.	.	.	.	.	.	.	12
46.112	.	2	.	.	.	.	.	.	22	.	.	18	3	.	.	.	.	.	.	.	.	.	.	45
46.114	.	.	.	.	.	.	.	.	2	.	.	1	1	.	.	1	.	.	.	.	.	.	.	5
46.116	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
46.118	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
46.120	.	1	.	.	.	.	.	.	1	.	.	3	1	.	.	2	.	.	.	.	.	.	.	8
46.122	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	2	.	.	5
46.124	.	.	.	.	.	.	.	.	.	.	1	1	2	.	.	.	.	.	.	.	.	.	.	4
46.126	.	4	.	.	.	.	.	.	5	.	.	3	.	1	.	1	.	1	.	.	.	.	.	15
46.128	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	3
46.130	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2
46.132	.	.	.	.	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	1	.	.	4
46.134	.	.	.	.	1	.	2	.	1	.	.	10	6	7	.	.	.	.	.	45	18	1	.	91
46.135	.	2	.	.	.	.	1	1	1	.	11	1	6	45	.	.	.	4	.	48	23	.	.	143
46.137	.	12	.	.	.	.	.	5	.	.	13	132	76	2	.	.	.	.	.	.	32	4	.	276
46.139	.	2	.	.	.	.	.	.	.	.	.	2	3	1	.	.	.	.	.	.	1	.	.	9
46.141	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	.	.	.	.	3	.	.	7
46.147	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	2	.	.	4
46.149	.	.	.	.	.	.	.	.	2	.	.	.	2	.	.	.	.	.	.	.	.	.	.	4
46.151	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1
46.153	.	1	.	.	.	.	.	.	1	.	.	14	.	.	.	.	.	.	.	.	.	.	.	16
46.155	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
46.157	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
46.163	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
46.165	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	1	.	.	3

APPENDIX TABLE 1.—Summary of occurrences and numbers of larvae of 23 categories, limited in distribution to a broad coastal band or around offshore islands or banks.—*Continued.*

STATION NUMBER	Engraulis ringens	Gobiidae	Albula vulpes	Etrumeus acuminatus	Opisthonema sp.	Sardinops sagax	Engraulidae (other)	Synodontidae	Bothus leopardinus	Citharichthys spp.	Cyclopsetta sp.	Syacium ovale	Symphurus spp.	Carangidae	Eucinostomus sp.	Labridae	Mugilidae	Polynemidae	Pomacentridae	Sciaenidae	Scorpaenidae	Serranidae	Carapidae	Total: 23 categories
46.171	.	2	.	3	.	64	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	69
46.173	.	2	.	.	.	2	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	5
46.175	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
46.177	.	.	.	.	.	21	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	21
46.179	.	3	.	1	.	81	.	.	.	21	.	.	.	.	.	1	.	.	.	.	.	.	.	107
46.181	.	.	.	3	.	5	.	.	.	8	.	.	1	.	.	.	.	.	.	.	.	.	.	20
46.185	.	.	.	.	.	.	.	.	.	4	.	.	1	.	.	.	.	.	.	.	.	.	.	5
46.187	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	5	.	6
CRUISE 47																								
47.001	.	9	.	.	.	.	.	4	.	.	.	3	3	4	.	.	.	.	.	.	1	.	.	24
47.005	.	46	.	.	.	.	.	5	.	.	.	11	2	2	.	.	.	.	.	.	3	.	.	69
47.008	.	35	.	.	.	.	.	2	3	5	.	2	3	1	1	.	.	.	.	.	3	.	1	56
47.011	.	11	.	.	.	.	.	.	.	.	1	.	1	11	.	.	.	.	.	.	1	.	.	25
47.019	.	36	2	.	.	.	5	7	1	.	3	5	9	5	4	4	7	2	2	.	4	7	.	103
47.022	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	3
47.025	.	5	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	1	.	.	.	.	8
47.028	.	24	.	.	.	.	.	.	.	.	.	3	12	.	.	.	.	.	.	.	1	.	.	40
47.032	.	6	.	.	.	.	.	.	.	.	.	4	2	.	.	.	.	.	.	.	5	.	.	17
47.034	.	2	.	.	.	.	.	.	.	.	.	3	9	3	.	.	.	.	.	.	10	.	.	27
47.035	.	.	.	.	.	.	.	.	.	.	.	.	1	5	.	.	.	.	.	.	6	.	.	12
47.040	.	19	.	.	.	.	25	3	.	2	.	3	1	6	7	6	3	.	1	1	10	17	.	107
47.049	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.053	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2
47.057	.	5	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	7
47.061	.	2	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	2	.	.	6
47.065	.	3	.	.	.	.	.	.	.	1	1	.	4	4	.	1	2	.	1	.	1	.	1	19
47.069	1	6	.	.	.	.	.	1	.	.	1	3	2	.	.	1	.	.	.	.	.	.	.	15
47.070	.	2	.	.	.	.	.	.	.	2	.	1	1	.	.	.	2	.	.	.	.	.	.	8
47.074	.	13	.	.	.	.	.	.	.	9	.	1	1	.	.	.	.	.	.	1	1	3	.	29
47.078	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	2
47.082	26	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26
47.086	127	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	127
47.090	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.097	250	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	252
47.099	48	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	.	.	.	59
47.101	222	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	222
47.103	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.105	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.107	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	7
47.109	293	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	293
47.113	35	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	35
47.124	99	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	99
47.128	96	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	96
47.132	43	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	43
47.139	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
47.141	12	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
47.147	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.152	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.173	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
47.175	13	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13
47.177	4	5	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	10

APPENDIX TABLE 4.—Summary of occurrences and number of larvae of 23 categories, limited in distribution to a broad coastal band or around offshore islands or banks.—*Continued.*

STATION NUMBER	Engraulis ringens	Gobiidae	Albula vulpes	Etrumeus acuminatus	Opisthonema sp.	Sardinops sagax	Engraulidae (other)	Synodontidae	Bothus leopardinus	Citharichthys spp.	Cyclopsetta sp.	Syacium ovale	Symphurus spp.	Carangidae	Eucinostomus sp.	Labridae	Mugilidae	Polynemidae	Pomacentridae	Sciaenidae	Scorpaenidae	Serranidae	Carapidae	Total: 23 categories
47.179	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.181	1	3	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	3	1	.	10
47.185	13	1	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	1	1	1	.	19
47.189	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	2
47.197	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	11
47.201	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	2
47.229	.	3	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	2	.	.	7
47.233	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	4	.	.	6
47.237	.	1	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	2	.	.	5
47.240	.	5	.	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.	.	.	1	.	.	9
47.242	.	4	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	1	.	.	7
47.244	.	.	.	.	.	.	.	.	1	.	.	2	1	.	.	.	.	.	.	.	.	1	.	5
47.246	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
47.250	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	3
47.254	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	2	.	.	.	1	.	8
47.258	.	5	.	.	.	.	.	4	.	10	.	3	4	16	.	.	2	.	.	1	36	3	.	84
47.268	.	.	.	.	.	.	.	1	.	1	2	.	9	.	.	.	.	.	.	.	5	3	.	21
47.272	.	1	.	.	.	.	.	.	.	.	1	.	4	3	.	.	.	.	.	.	2	2	.	13
47.276	.	8	.	.	.	.	.	.	.	.	.	4	2	.	.	3	.	.	.	.	.	.	.	17
47.278	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	2	.	3
47.283	.	1	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	3
47.286	.	1	.	.	.	.	.	.	1	.	.	1	5	.	.	1	.	.	.	.	.	.	.	9
47.288	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	3
47.290	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
47.292	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
47.295	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
47.301	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
47.304	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2
47.306	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	4	.	5
47.310	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	.	5
47.314	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2
47.322	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
47.330	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
47.334	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
47.349	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
47.357	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
47.436	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
47.446	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
47.450	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
47.466	.	.	.	.	.	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	3
47.470	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.	2
47.501	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
47.504	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	2
47.507	.	.	.	.	.	.	.	.	.	.	.	3	1	1	.	.	.	.	.	.	.	.	.	5
47.509	.	.	.	.	.	.	.	.	3	.	.	2	.	.	.	.	.	.	.	.	.	.	.	5
47.511	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	2
47.513	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1
47.515	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
47.517	.	1	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	3
47.520	.	8	.	.	.	.	.	.	.	.	.	13	8	.	.	1	.	.	.	.	13	.	.	43
47.523	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	1	.	.	.	.	2	1	.	7
47.525	.	.	.	.	.	.	.	.	1	.	.	3	4	.	.	.	.	.	.	.	1	.	.	9
47.527	.	7	7	.	83	.	1	23	36	.	1	180	142	69	3	.	.	.	.	15	1	.	.	568

APPENDIX TABLE 5.—Numbers and kinds of eel leptocephali (Anguilliformes) obtained on the second multivessel EASTROPAC survey (EASTROPAC II), tabulated by family for all positive hauls.

STATION NUMBER	Eel leptocephali	Congridae	Moringuidae	Muraenidae	Nemichthyidae	Ophichthidae	Serrivomeridae	Xenocongridae	Family unknown
45 .018	2	.	.	.	2	.	.	.	.
45 .023	1	.	.	.	1	.	.	.	.
45 .030	1	.	.	.	.	1	.	.	.
45 .058	1	.	.	.	.	1	.	.	.
45 .063	1	.	.	.	.	.	.	.	1
45 .065	2	.	.	.	.	2	.	.	.
45 .067	2	.	.	.	.	2	.	.	.
45 .071	1	.	.	.	.	1	.	.	.
45 .073	1	.	.	.	.	.	.	.	1
45 .140	2	.	.	.	1	.	.	.	1
45 .313	1	.	.	.	.	1	.	.	.
45 .362	1	1	.	.	.	.	.	.	.
45 .365	12	4	1	.	.	7	.	.	.
45 .367	3	1	.	.	.	.	.	.	2
45 .371	1	.	.	.	.	1	.	.	.
45 .379	1	.	.	.	1	.	.	.	.
46 .032	1	1	.	.	.	.	.	.	.
46 .034	1	.	.	.	.	.	.	.	1
46 .046	2	.	.	.	.	.	.	.	2
46 .065	1	1	.	.	.	.	.	.	.
46 .077	1	1	.	.	.	.	.	.	.
46 .086	2	.	.	.	1	.	.	1	.
46 .098	1	.	.	.	.	.	.	.	1
46 .106	1	.	.	.	1	.	.	.	.
46 .108	1	.	.	.	1	.	.	.	.
46 .110	2	.	.	1	.	1	.	.	.
46 .112	1	.	.	.	1	.	.	.	.
46 .114	1	.	.	1	.	.	.	.	.
46 .120	1	.	.	.	.	1	.	.	.
46 .122	1	1	.	.	.	.	.	.	.
46 .124	2	.	.	.	.	2	.	.	.
46 .128	1	1	.	.	.	.	.	.	.
46 .130	2	2	.	.	.	.	.	.	.
46 .134	2	.	.	.	.	2	.	.	.
46 .135	3	.	.	.	.	3	.	.	.
46 .137	1	1	.	.	.	.	.	.	.
46 .139	4	2	.	.	.	2	.	.	.
46 .143	1	.	.	.	.	1	.	.	.
46 .145	2	1	.	1	.	.	.	.	.
46 .153	1	.	.	.	1	.	.	.	.
46 .155	1	.	.	.	1	.	.	.	.
46 .157	1	.	.	.	1	.	.	.	.
46 .161	1	.	.	.	.	.	.	.	1
46 .165	1	.	.	.	1	.	.	.	.
46 .169	1	.	.	.	1	.	.	.	.
46 .177	1	.	.	.	.	.	.	1	.
47 .001	3	1	.	.	.	2	.	.	.
47 .008	1	1	.	.	.	.	.	.	.
47 .011	3	2	.	.	.	1	.	.	.
47 .019	11	4	.	2	.	5	.	.	.
47 .028	2	.	1	.	.	1	.	.	.
47 .032	1	.	1	.	.	.	.	.	.
47 .035	1	1	.	.	.	.	.	.	.
47 .040	6	.	.	.	.	3	.	.	3
47 .049	2	.	.	.	.	2	.	.	.
47 .053	2	.	.	.	.	.	.	1	1
47 .069	1	.	.	.	.	1	.	.	.
47 .070	1	.	.	.	.	1	.	.	.
47 .107	1	.	.	.	.	1	.	.	.
47 .179	1	.	.	.	.	1	.	.	.
47 .197	1	.	.	.	.	1	.	.	.
47 .217	1	1	.	.	.	.	.	.	.
47 .229	1	1	.	.	.	.	.	.	.
47 .233	1	.	.	.	1	.	.	.	.
47 .242	1	.	.	.	1	.	.	.	.
47 .244	1	1	.	.	.	.	.	.	.
47 .254	1	1	.	.	.	.	.	.	.
47 .258	4	2	.	1	.	.	.	.	1
47 .268	1	.	.	.	.	1	.	.	.
47 .276	1	1	.	.	.	.	.	.	.
47 .283	1	.	.	.	.	1	.	.	.
47 .286	1	.	.	.	1	.	.	.	.
47 .297	3	1	.	.	.	.	.	.	2
47 .304	2	.	.	.	1	.	.	1	.
47 .314	3	2	.	.	1	.	.	.	.
47 .438	2	.	.	.	2	.	.	.	.
47 .478	1	.	.	.	.	1	.	.	.
47 .504	1	.	.	.	.	1	.	.	.
47 .509	1	1	.	.	.	1	.	.	1
47 .525	3	3	.	.	.	.	.	.	.
47 .527	7	2	.	.	.	5	.	.	.

APPENDIX TABLE 6.—Numbers and kinds of lophiiform larvae obtained on the second multivessel EASTROPAC survey (EASTROPAC II), tabulated by family for all positive hauls.

STATION NUMBER	Caulophrynidae	Centrophrynidae	Ceratiidae	Gigantactinidae	Himantolophidae	Linophrynidae	Melanocoetidae	Oneirodidae	Unidentified Ceratioidei	Antennariidae	Lophiidae
45 .037	.	.	.	.	.	1	.	.	.	.	.
45 .039	.	.	.	.	.	.	.	.	1	.	.
45 .044	.	.	.	1	.	.	.	.	.	.	.
45 .046	.	.	.	1	.	.	.	.	.	.	.
45 .048	.	.	.	.	.	.	.	1	1	.	.
45 .050	.	.	.	.	1	.	.	.	1	.	.
45 .051	.	.	.	.	.	.	.	1	1	.	.
45 .053	.	.	.	.	.	.	.	1	.	.	.
45 .054	.	.	.	.	.	.	.	1	.	.	.
45 .056	.	.	.	1	.	.	1	1	.	.	.
45 .058	.	.	.	1	1	.	.	1	.	.	.
45 .060	.	.	.	.	.	.	.	1	.	.	.
45 .063	.	.	.	1	.	.	1	.	.	.	.
45 .065	.	.	.	.	.	.	1	.	3	.	.
45 .067	.	.	.	2	2	.	.	.	1	.	.
45 .078	.	.	.	.	.	.	.	1	.	.	.
45 .110	.	.	.	.	.	.	.	1	.	.	.
45 .127	.	.	.	.	.	.	.	1	.	.	.
45 .131	.	.	.	1	.	.	.	.	.	.	.
45 .171	.	.	.	1	.	.	.	.	.	.	.
45 .175	.	.	.	.	.	1	.	.	.	.	.
45 .309	.	.	.	.	1	.	.	.	.	.	.
45 .319	.	.	.	.	.	.	.	1	1	.	.
45 .321	.	.	.	.	.	.	.	.	1	.	.
45 .325	.	1	.	.	.	.	.	.	1	.	.
46 .028	1	.	.	.	.	.	1	.	.	.	.
46 .034	.	.	.	.	.	.	.	1	1	.	.
46 .044	.	.	.	.	.	.	.	.	1	.	.
46 .046	.	.	.	1	1	.	.	2	.	.	.
46 .048	.	.	.	.	.	.	1	.	.	.	.
46 .052	.	.	.	.	.	.	.	1	.	.	.
46 .057	.	.	.	.	.	.	.	1	.	.	.
46 .059	.	.	.	.	.	.	.	.	1	.	.
46 .086	.	.	.	.	.	.	.	1	.	.	.
46 .088	.	.	.	.	.	.	1	.	.	.	.
46 .094	.	.	.	.	.	.	.	.	1	.	.
46 .098	.	.	1	.	.	.	.	.	.	.	.
46 .100	.	.	.	1	.	.	.	.	.	.	.
46 .102	.	.	.	1	.	.	.	2	.	.	.
46 .104	.	.	.	.	.	.	.	.	1	.	.
46 .108	.	.	.	.	.	.	1	.	.	.	.
46 .110	.	.	.	.	.	.	1	.	.	.	.
46 .112	.	.	.	.	.	.	.	2	.	.	.
46 .114	.	.	.	.	.	.	1	.	.	.	.
46 .122	.	.	.	.	.	.	.	.	1	.	.
46 .126	.	.	.	.	.	.	4	.	.	.	.
46 .128	.	.	.	.	.	.	2	.	1	.	.
46 .132	.	.	.	.	.	.	.	.	.	1	.
46 .139	.	.	.	.	.	.	1	.	.	.	.
46 .145	.	.	.	.	.	.	.	.	.	.	1
46 .153	.	.	.	.	.	.	.	1	.	.	.
46 .155	.	.	.	.	.	.	.	1	.	.	.
46 .159	.	.	.	.	.	.	1	3	.	.	.
46 .161	.	.	2	1	.	.	.	1	.	.	.
46 .163	.	.	.	.	.	.	2	1	.	.	.
46 .165	1	.	.	1	.	.	1	.	.	.	.
46 .167	.	.	.	.	.	.	.	1	.	.	.

STATION NUMBER	Caulophrynidae	Centrophrynidae	Ceratiidae	Gigantactinidae	Himantolophidae	Linophrynidae	Melanocoetidae	Oneirodidae	Unidentified Ceratioidei	Antennariidae	Lophiidae
46 .169	.	.	.	.	.	.	1	.	.	.	.
47 .001	.	.	.	.	.	1	.	.	.	.	.
47 .005	.	.	.	.	.	.	.	1	1	.	.
47 .008	.	.	.	.	.	2	.	1	.	.	.
47 .011	.	.	.	.	.	3	.	.	.	.	.
47 .019	.	.	.	.	.	.	2	2	.	.	.
47 .025	.	.	.	.	.	.	.	2	.	.	.
47 .028	.	.	.	.	.	4	.	2	.	.	.
47 .032	.	.	.	.	.	.	2	.	.	.	.
47 .034	.	.	.	.	.	.	.	1	.	.	.
47 .035	.	.	.	.	.	1	.	.	2	.	.
47 .040	.	.	1	.	.	.	.	.	.	.	.
47 .049	.	.	.	.	.	.	.	1	.	.	.
47 .053	.	.	1	.	.	.	.	5	.	.	.
47 .057	.	.	.	1	.	.	.	.	.	.	.
47 .061	.	.	.	.	.	.	.	1	.	.	.
47 .074	.	.	.	.	.	2	.	.	.	.	.
47 .090	.	.	.	.	.	1	.	.	.	.	.
47 .141	.	.	.	.	.	1	.	.	.	.	.
47 .177	.	.	.	.	.	1	.	.	.	.	.
47 .197	.	.	.	.	.	1	.	.	.	.	.
47 .201	.	.	.	.	.	1	.	.	.	.	.
47 .213	.	.	.	.	.	.	.	4	.	.	.
47 .217	.	.	.	.	.	.	.	4	.	.	.
47 .225	.	.	.	.	.	.	.	3	2	.	.
47 .229	.	.	.	.	1	1	.	1	1	.	.
47 .240	.	.	.	.	.	.	.	.	1	.	.
47 .242	.	.	.	.	.	2	1	.	.	.	.
47 .244	.	.	.	.	.	.	4	6	.	.	.
47 .246	.	.	.	.	.	.	1	1	.	.	.
47 .250	.	.	.	.	.	1	.	2	.	.	.
47 .254	.	.	.	.	.	.	.	.	1	.	.
47 .268	.	.	.	.	.	1	.	.	.	.	.
47 .276	.	.	.	.	.	1	.	.	.	.	.
47 .283	.	.	.	.	.	.	1	.	.	.	.
47 .286	.	.	.	.	.	.	2	.	.	.	.
47 .292	.	.	.	.	.	.	.	1	.	.	.
47 .295	.	.	.	.	.	.	.	4	.	.	.
47 .297	.	.	.	.	.	.	.	1	.	.	.
47 .306	.	.	.	.	.	.	.	.	4	.	.
47 .310	.	.	.	6	.	2	1	5	2	.	.
47 .322	.	.	3	.	.	.	1	1	.	.	.
47 .326	.	.	.	.	.	4	.	.	.	.	.
47 .351	.	.	.	.	.	2	.	.	.	.	.
47 .357	.	.	.	.	.	.	1	.	.	.	.
47 .450	.	.	.	1	.	.	.	.	.	.	.
47 .454	.	.	.	.	.	.	.	.	1	.	.
47 .486	.	.	.	1	1	.	.	2	.	.	.
47 .490	.	.	.	4	.	.	.	2	1	.	.
47 .498	.	.	.	.	1	.	.	.	.	.	.
47 .501	.	.	.	.	.	.	1	.	.	.	.
47 .504	.	.	.	.	.	.	1	.	.	.	.
47 .507	.	.	.	.	.	.	1	.	.	.	.
47 .511	.	.	.	.	.	.	1	.	.	.	.
47 .513	.	.	.	.	.	.	1	.	.	.	.
47 .523	.	.	.	.	.	.	1	.	.	.	.
47 .525	.	.	.	.	.	.	1	.	.	.	.

APPENDIX TABLE 7A.—Counts of fish larvae, tabulated by family, for all stations occupied by *Oceanographer* on zig-transect.

STATION NUMBER	Myctophidae	Gonostomatidae	Bathylagidae	Clupeidae	Engraulidae	Sternoptychidae	Chauliodontidae	Idiacanthidae	Other Stomiatoidei	Paralepididae	Scopelosauridae	Melamphaidae	Bregmacerotidae	Exocoetidae	Bramidae	Chiasmodontidae	Coryphaenidae	Nomeidae	Scombridae	Other Identified Larvae	Unidentified Larvae	Disintegrated Larvae	Total Fish Larvae
OP .001	8	.	.	.	7	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	17
OP .002	2	.	.	.	200	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	202
OP .003	4	.	.	.	74	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	79
OP .005	32	9	3	.	.	.	1	.	.	.	.	2	.	.	.	.	.	3	.	.	.	2	52
OP .007	50	19	11	.	.	.	1	.	.	.	.	.	.	.	.	2	.	3	.	.	.	2	88
OP .009	41	9	12	.	.	1	1	.	.	.	.	18	.	.	.	8	.	1	.	.	.	.	91
OP .011	50	19	6	.	.	.	3	.	.	.	.	4	.	.	.	2	.	7	.	5	1	9	106
OP .013	70	22	20	.	.	.	11	.	.	.	.	3	.	.	.	2	.	3	.	1	.	.	132
OP .015	46	15	24	.	.	.	5	.	.	.	.	1	.	.	2	1	.	.	.	.	2	2	98
OP .017	13	1	1	.	.	5	.	.	.	.	.	2	.	.	.	2	.	1	.	2	.	2	29
OP .019	20	10	8	.	.	16	1	.	1	.	.	1	.	.	1	.	.	3	.	.	3	.	64
OP .021	10	7	4	.	.	6	.	.	.	.	.	2	.	.	.	.	.	4	.	.	1	2	36
OP .023	251	53	15	.	.	61	2	.	1	.	.	5	.	.	.	3	.	.	.	.	.	2	393
OP .025	206	31	8	.	.	19	.	.	2	.	.	3	.	.	.	1	.	3	.	1	.	1	275
OP .027	248	110	111	.	.	41	.	3	8	14	.	9	.	.	.	1	.	13	.	1	.	30	589
OP .029	168	146	153	.	.	26	.	1	18	34	.	5	.	.	1	.	.	12	.	2	1	56	623
OP .032	321	154	213	.	1	54	2	3	17	79	2	16	.	.	.	3	.	7	.	1	1	12	886
OP .036	543	2047	487	.	1	36	.	.	18	57	.	12	.	.	.	.	.	10	.	2	.	25	3238
OP .040	113	126	176	.	.	6	.	.	14	9	.	3	.	.	.	1	.	11	.	1	.	8	468
OP .044	100	64	38	.	.	5	.	1	12	7	.	5	.	.	.	8	.	7	.	17	.	1	265
OP .048	230	103	119	.	.	47	.	.	24	54	20	13	.	.	2	1	.	4	.	18	.	97	732
OP .052	101	52	51	.	.	12	.	.	1	6	34	3	.	.	.	3	1	12	.	14	5	20	315
OP .056	62	20	108	.	.	4	.	1	5	40	26	10	.	.	1	.	1	3	.	5	5	30	321
OP .060	43	26	65	.	.	8	.	1	8	8	5	7	.	3	.	2	1	1	.	2	2	3	185
OP .064	387	51	96	.	.	17	.	.	17	26	21	17	.	.	.	2	1	3	.	7	.	10	655
OP .068	119	40	54	.	.	34	.	.	4	16	11	7	.	.	.	6	.	.	.	12	.	3	306
OP .072	109	7	30	.	.	13	.	1	.	9	1	4	.	.	1	4	.	.	.	4	.	4	187
OP .076	86	22	18	.	.	8	.	.	7	18	1	6	.	.	3	1	.	1	.	3	1	5	180
OP .080	127	67	49	.	.	20	.	.	5	13	2	8	.	.	1	2	.	8	.	1	.	4	307
OP .084	105	12	46	.	.	7	.	1	5	19	.	8	.	.	.	1	.	1	.	3	.	14	222
OP .088	70	28	34	.	.	29	.	1	2	38	.	3	.	.	.	3	.	2	.	3	1	7	221
OP .092	17	6	28	.	.	2	.	.	2	7	.	1	.	.	.	1	.	1	.	9	.	1	75
OP .096	64	7	6	.	.	15	.	.	2	19	2	.	.	.	.	.	.	.	.	2	5	2	124
OP .100	92	4	6	.	.	.	.	.	2	5	4	.	.	.	.	.	.	.	.	1	.	.	114
OP .104	60	16	2	7	.	3	.	2	7	3	.	1	.	.	.	.	.	.	.	2	3	3	109
OP .108	95	44	31	.	.	7	.	7	6	28	3	2	.	.	1	.	.	.	.	1	4	6	235
OP .112	320	100	75	.	.	6	.	.	1	11	4	15	.	.	1	1	.	4	.	8	.	6	552
OP .116	383	123	43	.	.	18	.	.	.	23	2	11	.	.	3	.	.	2	.	7	1	5	621
OP .120	110	6	6	.	.	27	.	1	.	2	.	5	.	.	.	.	.	.	.	3	2	3	165
OP .124	296	3	4	.	.	67	2	1	1	.	.	3	.	.	.	.	1	4	.	4	.	.	386
OP .128	1325	181	20	.	.	133	3	2	4	5	.	4	.	1	.	.	.	2	.	5	1	11	1697
OP .132	1454	229	15	.	.	115	3	.	5	5	.	3	.	.	.	.	1	8	.	7	1	10	1856
OP .136	343	14	4	.	.	17	.	1	1	.	.	.	.	5	.	.	.	5	3	3	.	12	408
OP .138	411	9	15	.	.	54	3	.	3	.	.	5	.	.	.	.	.	4	2	1	.	3	510
OP .155	372	37	52	.	.	20	1	.	2	.	.	5	.	.	.	1	1	1	2	3	.	25	522
OP .160	220	152	27	.	.	11	7	.	4	.	.	2	.	5	3	2	1	5	3	33	.	35	510
OP .162	255	155	6	.	.	.	.	.	.	1	.	4	.	2	2	.	.	15	48	31	1	5	525
OP .164	19	10	1	.	.	3	.	.	.	.	.	1	.	.	.	1	.	9	11	2	.	4	61
OP .166	4	2	1	.	.	3	.	.	.	.	.	2	.	.	.	.	.	2	.	3	.	1	18
OP .168	131	18	62	730	477	.	.	.	.	.	.	2	470	.	.	.	.	.	13	704	11	5	4567

APPENDIX TABLE 7B.—Myctophid larvae, tabulated by genus or species, stations occupied by *Oceanographer* on zig-transect.

STATION NUMBER	Benthosema pterota panamense	Ceratoscopelus townsendi	Diaphus spp.	Diogenichthys laternatus	Gonichthys tenuiculus	Hygophum atratum	Hygophum proximum	Lampadena spp.	Lampanyctus spp.	Lepidophanes sp.	Lobianchia sp.	Loweina rara	Myctophum aurolaternatum	Myctophum nitidulum	Myctophum sp.	Notolychnus valdiviae	Notoscopelus resplendens	Protomyctophum sp.	Symbolophorus evermanni	Triphoturus spp.	Unidentified Myctophids	Disintegrated Myctophids	Total Myctophids
OP .001	.	.	.	.	.	.	.	.	6	.	.	.	.	.	.	.	.	.	.	1	.	1	8
OP .002	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	2
OP .003	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	4
OP .005	.	.	.	2	.	.	.	.	21	.	.	.	.	.	.	.	.	.	1	7	.	1	32
OP .007	.	.	1	8	.	.	.	.	12	.	.	.	.	.	.	.	1	.	16	12	.	.	50
OP .009	.	.	1	8	.	.	.	.	15	.	.	.	.	.	.	.	.	.	4	3	4	6	41
OP .011	.	.	.	10	.	.	.	.	11	.	.	.	.	.	.	.	.	.	7	13	2	7	50
OP .013	.	2	3	15	.	.	.	.	18	.	.	.	.	.	.	.	5	.	8	13	5	1	70
OP .015	.	.	.	5	1	2	.	.	5	.	.	.	.	.	.	.	2	.	19	5	5	2	46
OP .017	.	.	.	3	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	1	.	5	13
OP .019	.	.	.	5	.	1	.	.	3	.	.	.	.	.	.	.	.	.	7	3	1	.	20
OP .021	.	.	.	1	.	.	.	.	8	.	.	.	.	.	.	.	.	.	.	1	.	.	10
OP .023	.	.	.	188	1	.	.	.	47	.	.	.	.	.	.	.	.	.	1	10	4	.	251
OP .025	.	.	.	180	.	.	.	.	21	.	.	.	.	.	.	.	.	.	.	5	.	.	206
OP .027	.	.	.	213	1	6	.	.	16	.	.	.	.	2	.	.	.	.	2	.	.	8	248
OP .029	.	.	.	113	1	4	.	.	12	.	.	.	.	10	.	.	1	.	2	1	4	20	168
OP .032	.	.	2	229	4	.	.	.	12	.	.	.	3	25	.	.	1	.	5	27	.	13	321
OP .036	.	.	.	487	1	.	.	.	19	.	.	.	.	7	.	.	.	.	.	24	.	5	543
OP .040	.	.	.	65	.	.	.	.	25	.	.	.	.	17	.	.	.	.	.	4	.	2	113
OP .044	.	.	1	43	3	.	.	.	4	.	.	.	4	42	.	.	3	.	.	.	.	.	100
OP .048	.	.	1	51	5	.	.	.	91	.	.	.	5	47	.	.	3	.	.	9	2	16	230
OP .052	.	.	2	51	.	1	.	.	27	.	.	.	.	11	.	.	.	.	.	2	1	6	101
OP .056	.	.	1	18	1	.	.	.	5	.	.	.	.	15	.	1	.	.	.	2	5	14	62
OP .060	.	.	3	11	.	.	.	.	7	.	.	.	.	18	.	.	.	.	.	2	.	2	43
OP .064	.	.	5	253	3	.	.	.	65	.	.	.	1	38	.	.	6	.	.	11	.	5	387
OP .068	.	.	4	24	5	.	.	.	24	.	.	.	5	27	1	.	14	1	1	3	2	8	119
OP .072	.	.	.	16	5	.	.	.	23	.	.	.	1	47	.	.	3	.	.	1	.	13	109
OP .076	.	.	5	24	3	.	.	.	3	.	.	.	.	31	.	.	7	.	.	5	.	8	86
OP .080	.	.	5	46	1	.	.	.	32	.	.	.	1	30	.	.	7	.	.	5	.	.	127
OP .084	.	.	.	55	3	.	.	.	15	.	.	.	1	15	.	1	1	1	.	1	.	12	105
OP .088	.	.	5	26	1	.	.	.	20	.	.	.	1	5	.	.	4	.	4	2	.	2	70
OP .092	.	.	.	6	.	.	.	.	6	.	.	.	.	2	.	.	2	.	.	.	1	.	17
OP .096	.	.	3	41	2	.	.	.	5	.	.	.	.	3	.	.	2	1	.	7	.	.	64
OP .100	.	.	2	77	.	.	.	.	7	.	.	.	.	.	.	.	1	.	.	5	.	.	92
OP .104	.	.	1	20	.	.	.	.	15	.	.	.	.	14	.	.	1	.	1	7	.	1	60
OP .108	.	.	4	32	4	1	.	.	11	.	1	.	1	26	.	2	4	.	.	4	.	5	95
OP .112	.	.	4	256	.	.	1	.	39	.	.	.	3	1	.	2	2	.	3	4	.	5	320
OP .116	.	.	.	347	.	.	1	.	16	.	.	.	6	5	.	3	1	.	1	.	3	.	383
OP .120	.	.	.	97	1	.	.	.	1	.	.	.	2	3	.	2	1	.	1	1	.	1	110
OP .124	.	.	.	265	.	.	.	.	14	.	.	.	3	2	.	6	2	1	1	2	.	.	296
OP .128	.	.	11	188	9	.	.	.	88	.	.	.	9	1	.	5	.	1	9	2	1	11	1325
OP .132	.	.	11	300	2	.	.	.	122	.	.	.	15	1	.	2	1	4	3	.	.	3	1454
OP .136	.	.	.	338	1	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	343
OP .138	.	.	.	403	.	.	.	.	7	.	.	.	1	.	.	.	.	.	.	.	.	.	411
OP .155	.	.	.	346	.	.	.	.	18	.	.	.	1	.	.	.	.	.	.	.	.	7	372
OP .160	.	.	2	135	3	.	.	.	65	.	.	.	.	.	.	.	.	.	.	.	.	15	220
OP .162	.	.	.	206	2	.	.	.	45	.	.	.	2	.	.	.	.	.	.	.	.	.	255
OP .164	.	.	.	19	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
OP .166	.	.	.	2	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	4
OP .168	43	.	.	86	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	131

APPENDIX TABLE 7C.—Counts of selected categories of fish larvae, tabulated by station, for *Oceanographer* on zig-transect.

STATION NUMBER	Bathylagus nigrigenys	Leuroglossus stilbius urotranus	Cyclothone spp.	Ichthyococcus irregularis	Maurolicus muelleri	Vinciguerria lucetia	Bathophilus sp.	Stomias sp.	Scopelarchidae	Trachypteridae	Diplospinus multistriatus	Lepidopus sp.	Nealotus tripes	Carangidae	Gobiidae	Labridae	Sciaenidae	Scorpaenidae	Serranidae	Bothus leopardinus	Citharichthys spp.	Syacium ovale	Symphurus spp.	Total: selected categories
OP .001	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1
OP .002	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
OP .003	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	0
OP .005	3	.	1	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
OP .007	11	.	1	.	.	18	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30
OP .009	12	.	1	.	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21
OP .011	6	.	2	.	.	17	.	.	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	30
OP .013	20	.	3	.	.	19	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	43
OP .015	24	.	6	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	39
OP .017	1	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	3
OP .019	8	.	1	.	.	9	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
OP .021	4	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
OP .023	15	.	2	.	.	51	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	69
OP .025	8	.	1	.	.	30	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	42
OP .027	44	67	.	.	.	110	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	225
OP .029	52	101	2	.	.	144	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	302
OP .032	69	144	1	.	.	152	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	368
OP .036	36	451	.	.	12046	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2535
OP .040	11	165	.	.	.	125	.	4	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	306
OP .044	24	14	.	.	.	60	.	2	1	.	.	1	1	.	2	1	1	4	.	1	.	.	3	115
OP .048	93	26	1	3	54	41	.	3	.	.	.	.	7	.	3	.	1	1	.	.	1	.	2	236
OP .052	50	1	1	2	5	43	.	.	.	1	.	.	6	.	1	.	.	1	1	.	.	.	.	112
OP .056	102	6	.	1	6	13	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	130
OP .060	65	.	.	.	17	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	91
OP .064	94	2	2	2	6	40	2	4	.	2	.	.	1	.	.	.	.	.	.	.	.	.	.	155
OP .068	44	10	1	.	.	38	.	1	.	.	.	.	4	.	.	.	.	1	.	1	.	.	.	100
OP .072	25	5	.	.	2	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	37
OP .076	18	.	2	1	2	17	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	41
OP .080	49	.	1	.	.	66	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	118
OP .084	45	1	3	.	4	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	61
OP .088	34	.	6	.	.	22	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	62
OP .092	28	.	3	.	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	41
OP .096	6	.	.	2	4	1	.	1	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	16
OP .100	6	.	.	.	1	3	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
OP .104	2	.	.	.	7	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	18
OP .108	31	.	1	2	19	22	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	76
OP .112	75	.	10	.	35	55	.	.	.	3	.	.	1	.	.	.	.	.	.	.	.	.	.	179
OP .116	43	.	9	2	12	100	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	169
OP .120	6	.	.	.	.	6	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	14
OP .124	4	.	.	.	.	3	.	.	1	.	.	.	1	.	.	1	.	.	.	.	.	.	.	10
OP .128	20	.	14	1	.	166	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	204
OP .132	15	.	12	3	.	214	.	4	1	.	.	.	.	.	.	.	.	.	.	1	.	2	.	252
OP .136	4	.	.	.	.	14	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	20
OP .138	15	.	.	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	24
OP .155	52	.	.	.	.	37	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	1	92
OP .160	27	.	.	.	.	152	.	.	1	.	.	.	.	.	16	.	.	.	.	4	.	4	3	207
OP .162	6	.	3	.	.	152	.	.	1	.	.	.	.	1	18	.	.	1	1	1	.	.	5	189
OP .164	1	.	.	.	.	10	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	12
OP .166	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
OP .168	6	.	.	.	.	18	.	.	.	.	.	.	.	353	2	.	31	3	24	.	5	31	149	622

APPENDIX TABLE 8.—Station data: latitude and longitude, date of collection, time of day, depth of haul, and standardized haul factor.

STATION NUMBER	Latitude	Longitude (W)	Date - Month and Day of 1967	Hour *	Depth of Haul	Standardized Haul Factor
CRUISE 45						
45 .016	20 00.0N	118 57.2	VIII- 7	1416-D	204	3.16
45 .018	19 15.7N	118 56.0	VIII- 8	0127-N	214	3.41
45 .020	18 34.8N	118 59.0	VIII- 8	0835-D	197	3.02
45 .021	18 14.8N	118 58.3	VIII- 8	1216-D	212	3.54
45 .023	17 41.0N	119 01.8	VIII- 8	2110-N	214	3.48
45 .024	17 19.9N	119 01.5	VIII- 9	0115-N	213	2.95
45 .026	16 31.0N	119 02.8	VIII- 9	0904-D	175	2.51
45 .028	16 11.3N	119 03.3	VIII- 9	1349-D	179	2.80
45 .030	15 48.5N	119 05.3	VIII- 9	1830-NT	201	3.35
45 .032	15 10.5N	119 04.0	VIII-10	0020-N	194	3.15
45 .034	14 34.2N	119 03.2	VIII-10	0636-DT	210	3.44
45 .035	14 11.2N	119 03.8	VIII-10	1255-D	183	2.79
45 .037	13 47.0N	119 04.0	VIII-10	1755-DT	198	3.53
45 .039	13 00.0N	119 03.6	VIII-10	2400-N	193	3.12
45 .041	12 31.0N	119 03.5	VIII-11	0534-NT	203	3.83
45 .043	11 54.5N	119 02.7	VIII-11	1338-D	177	2.74
45 .044	11 29.0N	119 00.5	VIII-11	1820-NT	207	3.56
45 .046	10 51.7N	119 02.2	VIII-11	0005-N	216	3.78
45 .048	10 15.7N	119 03.3	VIII-12	0601-DT	177	2.67
45 .050	09 34.3N	119 03.0	VIII-12	1446-D	201	3.54
45 .051	09 10.2N	118 59.5	VIII-12	2051-N	201	3.31
45 .053	08 46.6N	118 58.3	VIII-13	0105-N	203	3.19
45 .054	08 28.2N	118 57.0	VIII-13	0716-D	209	3.38
45 .056	07 53.2N	118 51.3	VIII-13	1505-D	203	3.28
45 .058	07 24.8N	118 47.2	VIII-13	2030-N	191	2.97
45 .060	06 50.0N	118 55.3	VIII-14	0151-N	211	3.40
45 .063	05 55.5N	118 56.5	VIII-14	1053-D	209	3.46
45 .065	05 23.2N	118 51.2	VIII-14	1901-NT	224	3.90
45 .067	04 53.5N	119 06.8	VIII-14	2345-N	222	3.88
45 .071	04 06.0N	119 15.3	VIII-15	0730-D	219	3.61
45 .073	03 34.2N	119 14.7	VIII-15	1536-D	210	3.79
45 .078	02 48.5N	119 11.0	VIII-15	0001-N	201	3.71
45 .083	02 02.0N	119 03.2	VIII-16	0640-DT	213	3.64
45 .086	01 33.8N	119 02.2	VIII-16	1229-D	212	4.18
45 .090	00 57.2N	119 04.5	VIII-16	1901-NT	209	4.15
45 .094	00 23.5N	119 01.5	VIII-17	0051-N	201	3.81
45 .098	00 13.5S	118 58.0	VIII-17	0740-D	205	3.50
45 .102	00 56.0S	118 51.0	VIII-17	1253-D	171	1.96
45 .106	01 42.2S	118 43.8	VIII-17	1901-NT	202	3.02
45 .110	02 22.0S	118 43.5	VIII-17	0036-N	196	4.02
45 .114	03 12.0S	118 43.2	VIII-18	0800-D	212	3.26
45 .117	03 38.0S	118 48.5	VIII-18	1237-D	222	3.52
45 .121	04 14.3S	118 50.0	VIII-18	1841-NT	191	2.86
45 .125	04 45.8S	118 53.0	VIII-19	0243-N	216	4.20
45 .127	05 10.0S	118 54.5	VIII-19	0745-D	192	3.31
45 .129	05 41.8S	118 54.9	VIII-19	1231-D	215	3.91
45 .131	06 19.5S	118 58.0	VIII-19	1831-NT	205	3.83
45 .133	06 57.8S	119 01.5	VIII-19	2344-N	219	3.47
45 .135	07 26.8S	119 04.0	VIII-20	0535-NT	199	3.56
45 .137	08 12.0S	119 06.3	VIII-20	1125-D	214	3.79
45 .139	08 47.8S	119 00.0	VIII-20	1718-DT	200	4.19
45 .140	09 44.7S	118 59.0	VIII-21	0016-N	217	3.95
45 .163	09 56.9S	111 59.5	VIII-23	1153-D	217	3.82
45 .165	09 17.0S	111 59.0	VIII-23	1758-NT	196	3.46
45 .167	08 38.0S	111 57.4	VIII-23	2346-N	211	3.80
45 .169	08 01.3S	111 54.3	VIII-24	0641-D	208	3.76
45 .171	07 22.4S	111 51.0	VIII-24	1211-D	208	3.00
45 .173	06 47.5S	111 53.5	VIII-24	1750-NT	201	3.18
45 .175	06 01.6S	111 56.7	VIII-24	2356-N	218	3.84
45 .177	05 21.1S	111 59.5	VIII-25	0607-DT	197	3.33
45 .179	04 44.3S	112 02.0	VIII-25	NOT QUANTITATIVE		
45 .183	04 10.0S	112 05.8	VIII-25	1757-NT	195	4.20
45 .187	03 30.0S	112 01.5	VIII-25	2336-N	208	3.70
45 .191	02 56.3S	111 57.5	VIII-26	0611-DT	185	3.12
45 .194	02 17.9S	111 59.0	VIII-27	1752-NT	208	3.44
45 .198	01 30.7S	111 53.1	VIII-27	2341-N	196	3.50
45 .202	00 48.6S	111 46.6	VIII-28	0625-DT	181	2.86
45 .206	00 17.2S	111 56.5	VIII-28	1203-D	212	3.66
45 .283	00 04.2N	111 59.3	IX- 2	1321-D	174	2.49
45 .287	00 32.5N	112 04.5	IX- 2	1926-N	237	4.99
45 .289	00 53.8N	112 03.3	IX- 2	0001-N	194	4.02
45 .293	01 26.2N	112 01.4	IX- 3	0621-DT	202	3.81
45 .297	02 07.9N	111 58.3	IX- 3	1209-D	207	3.30
45 .301	02 47.3N	112 02.0	IX- 3	1811-NT	217	3.95
45 .305	03 25.8N	112 00.3	IX- 3	2335-N	209	3.60
45 .309	04 08.6N	111 56.3	IX- 4	0601-DT	222	3.82
45 .313	04 55.0N	111 53.5	IX- 4	1154-D	192	2.93
45 .316	05 58.7N	111 57.8	IX- 4	1746-NT	215	3.53
45 .319	07 01.8N	112 05.4	IX- 5	0620-D	217	3.35
45 .321	07 40.2N	112 06.8	IX- 5	1149-D	194	2.77
45 .323	08 18.0N	112 01.0	IX- 5	1756-NT	194	2.58
45 .325	09 01.8N	111 54.8	IX- 5	0007-N	156	2.02
45 .329	10 18.7N	111 44.0	IX- 6	1150-D	202	2.86
45 .331	10 49.5N	111 39.5	IX- 6	1805-NT	175	2.45
45 .333	11 27.0N	111 57.0	IX- 6	2341-N	156	2.52
45 .335	12 05.7N	112 09.0	IX- 7	0605-DT	215	3.95
45 .337	12 27.8N	111 36.1	IX- 7	1146-D	207	3.17
45 .339	12 58.4N	111 14.3	IX- 7	1757-NT	216	3.11
45 .341	13 33.4N	110 50.0	IX- 7	0006-N	187	3.01
45 .343	13 56.3N	110 34.0	IX- 8	0805-D	193	2.79
45 .344	14 12.5N	110 23.0	IX- 8	1146-D	144	1.80
45 .345	14 38.2N	109 37.1	IX- 8	1841-N	135	1.71
45 .348	14 57.4N	109 04.3	IX- 8	2345-N	199	3.16
45 .350	15 16.0N	108 37.5	IX- 9	0535-DT	206	3.22
45 .352	15 45.0N	108 08.5	IX- 9	1141-D	217	3.56
45 .356	16 53.0N	107 03.0	IX- 9	2334-N	186	2.87
45 .358	17 20.5N	106 29.8	IX-10	0536-DT	208	3.40
45 .360	18 01.0N	105 41.0	IX-10	1248-D	216	3.68
45 .362	18 16.5N	105 20.5	IX-10	1828-N	199	3.27
45 .365	18 48.5N	104 44.0	IX-10	2351-N	207	3.48
45 .367	19 00.0N	104 50.0	IX-13	1455-D	212	3.57
45 .369	19 05.3N	105 09.2	IX-13	1925-N	209	3.53
45 .371	19 12.5N	105 40.5	IX-14	0024-N	203	3.33
45 .373	19 19.5N	106 13.8	IX-14	0601-D	221	3.63
45 .375	19 34.3N	106 57.2	IX-14	1148-D	184	2.74
45 .377	19 36.2N	107 37.6	IX-14	1810-NT	195	3.31
45 .379	19 38.5N	108 24.0	IX-14	2351-N	204	3.27
45 .381	19 41.7N	109 08.0	IX-15	0520-DT	192	2.82

APPENDIX TABLE 8.—Station data: latitude and longitude, date of collection, time of day, depth of haul, and standardized haul factor.—*Continued.*

STATION NUMBER	Latitude	Longitude (W)	Date - Month and Day of 1967	Hour *	Depth of Haul	Standardized Haul Factor
45 .383	19 48.0N	109 56.7	IX-15	1126-D	212	3.37
45 .385	19 53.0N	110 46.2	IX-15	1755-NT	200	3.07
45 .387	19 58.7N	111 25.2	IX-15	2328-N	206	3.22
CRUISE 46						
46 .002	16 14.0N	100 27.5	VIII-16	1801-NT	214	3.53
46 .004	15 48.5N	100 53.8	VIII-17	0032-N	195	2.60
46 .006	15 28.0N	101 18.0	VIII-17	0730-D	209	3.31
46 .007	15 13.0N	101 35.5	VIII-17	1150-D	262	3.91
46 .009	14 50.5N	102 02.0	VIII-17	1750-NT	202	2.98
46 .011	14 19.2N	102 38.0	VIII-17	2352-N	198	2.90
46 .013	13 56.0N	103 01.0	VIII-18	0541-D	211	3.39
46 .015	13 20.0N	103 27.0	VIII-18	1141-D	211	3.34
46 .017	12 53.0N	103 56.0	VIII-18	1741-NT	214	3.51
46 .019	12 16.0N	104 32.0	VIII-19	0052-N	208	2.99
46 .020	12 03.0N	104 46.0	VIII-19	0601-D	217	3.45
46 .022	11 26.0N	105 04.0	VIII-19	1136-D	192	2.39
46 .024	10 46.0N	105 08.0	VIII-19	1748-NT	216	3.37
46 .026	10 03.5N	105 02.0	VIII-19	2351-N	195	3.10
46 .028	09 31.0N	105 05.0	VIII-20	0551-D	211	3.65
46 .030	08 43.0N	105 03.0	VIII-20	1159-D	187	3.35
46 .032	08 07.0N	105 00.0	VIII-20	1733-NT	215	3.61
46 .034	07 22.0N	104 57.0	VIII-20	2351-N	216	3.58
46 .036	06 50.0N	104 54.0	VIII-21	0551-DT	126	1.85
46 .038	06 13.0N	104 47.0	VIII-21	1208-D	208	3.45
46 .040	05 39.0N	104 53.0	VIII-21	1749-NT	216	3.59
46 .042	04 52.0N	105 00.0	VIII-22	0041-N	208	3.57
46 .044	04 34.0N	105 02.0	VIII-22	0551-DT	214	3.56
46 .046	03 57.0N	105 04.0	VIII-22	1153-D	204	3.29
46 .048	03 33.0N	105 11.0	VIII-22	1748-NT	213	3.58
46 .050	02 50.0N	105 16.0	VIII-23	0011-N	204	3.35
46 .052	02 28.0N	105 15.0	VIII-23	0551-DT	210	3.28
46 .054	01 47.0N	105 12.0	VIII-23	1227-D	157	2.05
46 .055	01 29.0N	105 14.0	VIII-23	1809-N	159	2.09
46 .057	00 53.0N	105 19.0	VIII-23	2346-N	112	1.18
46 .059	00 24.0N	105 25.0	VIII-24	0606-D	84	.84
46 .061	00 20.0S	105 20.0	VIII-24	1159-D	161	2.36
46 .063	00 42.0S	105 15.0	VIII-24	1738-NT	219	3.73
46 .065	01 34.0S	105 08.0	VIII-25	0001-N	194	3.09
46 .067	02 00.0S	105 01.0	VIII-25	0541-DT	202	3.49
46 .069	02 47.7S	104 48.0	VIII-25	1204-D	261	3.43
46 .071	03 17.0S	104 55.0	VIII-25	1750-NT	199	3.16
46 .075	04 27.0S	105 00.0	VIII-28	1203-D	165	2.34
46 .077	05 01.0S	105 03.0	VIII-28	1750-NT	219	3.49
46 .079	01 04.0S	098 03.0	VIII-31	0321-N	170	2.19
46 .082	00 10.9S	098 02.0	VIII-31	1218-D	196	3.06
46 .084	00 10.0N	098 03.0	VIII-31	1808-N	208	3.41
46 .086	00 47.0N	098 04.0	IX- 1	0001-N	179	2.64
46 .088	01 12.0N	098 04.0	IX- 1	0546-D	217	3.96
46 .090	01 55.0N	098 05.0	IX- 1	1200-D	170	2.45
46 .092	02 21.0N	098 07.0	IX- 1	1729-NT	210	3.49
46 .094	03 08.0N	098 12.0	IX- 2	0001-N	196	2.97
46 .096	03 32.5N	098 14.5	IX- 2	0531-D	198	3.12
46 .098	04 20.0N	098 00.0	IX- 2	1208-D	198	3.14
46 .100	04 48.0N	098 04.0	IX- 2	1745-N	223	3.50
46 .102	05 36.0N	097 54.0	IX- 2	2341-N	210	3.21
46 .104	06 09.0N	097 45.0	IX- 3	0611-D	199	2.81
46 .106	06 56.4N	097 48.0	IX- 3	1211-D	213	3.45
46 .108	07 35.0N	098 00.0	IX- 3	1742-N	215	3.29
46 .110	08 25.0N	097 56.0	IX- 3	2351-N	209	3.94
46 .112	08 57.5N	097 51.0	IX- 4	0411-NT	212	3.93
46 .114	09 45.0N	097 48.0	IX- 4	1206-D	216	3.53
46 .116	10 25.0N	098 01.0	IX- 4	1742-N	221	3.86
46 .118	11 02.5N	098 04.5	IX- 5	0011-N	204	3.08
46 .120	11 28.0N	098 07.0	IX- 5	0422-NT	218	3.44
46 .122	12 17.9N	097 59.0	IX- 5	1238-D	201	3.10
46 .124	12 53.0N	098 03.0	IX- 5	1734-NT	220	3.68
46 .126	13 41.0N	098 03.0	IX- 6	0021-N	206	3.16
46 .128	14 09.0N	098 01.0	IX- 6	0416-NT	225	3.82
46 .130	14 56.0N	097 57.0	IX- 6	1211-D	199	3.11
46 .132	15 38.0N	098 01.0	IX- 6	1740-NT	213	2.60
46 .134	13 12.5N	091 51.0	IX-15	1141-D	214	3.54
46 .135	12 40.0N	092 03.0	IX-15	1701-NT	218	3.63
46 .137	11 48.0N	092 03.0	IX-15	2340-N	206	3.31
46 .139	11 08.0N	091 58.0	IX-16	0418-DT	199	2.90
46 .141	10 19.2N	091 54.0	IX-16	1151-D	204	3.23
46 .143	09 42.0N	091 58.0	IX-16	1732-N	218	3.57
46 .145	08 55.0N	092 02.0	IX-16	2349-N	177	2.55
46 .147	08 28.0N	092 05.0	IX-17	0419-DT	170	2.45
46 .149	07 44.0N	092 08.0	IX-17	1141-D	182	2.74
46 .151	07 01.0N	092 08.0	IX-17	1731-N	204	3.19
46 .153	06 13.0N	092 03.0	IX-17	2338-N	183	2.86
46 .155	05 40.0N	091 58.0	IX-18	0418-DT	224	3.88
46 .157	04 54.0N	091 52.0	IX-18	1141-D	205	3.17
46 .159	04 19.0N	091 56.0	IX-18	1731-N	219	3.58
46 .161	03 34.0N	091 56.0	IX-18	2339-N	217	3.47
46 .163	02 59.0N	092 00.0	IX-19	0418-DT	228	3.67
46 .165	02 13.0N	092 07.0	IX-19	1141-D	195	2.64
46 .167	01 39.0N	092 04.0	IX-19	1748-N	189	2.48
46 .169	00 54.0N	092 04.0	IX-20	0001-N	156	2.10
46 .171	00 23.0N	092 04.0	IX-20	0418-DT	216	3.71
46 .173	00 14.2S	092 03.0	IX-20	1141-D	194	2.95
46 .175	00 47.0S	092 03.0	IX-20	1731-N	207	3.45
46 .177	01 32.0S	092 06.0	IX-20	2339-N	197	3.33
46 .179	02 03.5S	092 07.0	IX-21	0416-DT	159	2.44
46 .181	02 49.6S	092 10.0	IX-21	1141-D	128	1.57
46 .183	03 27.0S	092 08.5	IX-21	1731-N	171	2.45
46 .185	04 09.5S	092 07.0	IX-21	2337-N	176	3.12
46 .187	04 46.0S	092 06.0	IX-22	0418-DT	222	3.42
46 .189	05 27.0S	092 05.0	IX-22	1211-D	205	3.42
CRUISE 47						
47 .001	05 36.0N	077 51.0	VII-31	1722-N	181	2.86
47 .005	06 03.0N	078 20.0	VIII- 1	2319-N	214	3.53
47 .008	06 24.0N	078 41.0	VIII- 2	0213-NT	164	2.33
47 .011	06 50.0N	079 16.0	VIII- 2	1046-D	175	2.60
47 .019	06 58.0N	080 54.0	VIII- 2	2306-N	156	1.88
47 .022	06 21.0N	080 41.0	VIII- 3	0331-DT	215	3.66
47 .025	05 41.0N	080 32.0	VIII- 3	0943-D	203	3.10
47 .028	04 51.0N	080 15.0	VIII- 3	1840-N	175	2.42

APPENDIX TABLE 8.—Station data: latitude and longitude, date of collection, time of day, depth of haul, and standardized haul factor.—*Continued.*

STATION NUMBER	Latitude	Longitude (W)	Date - Month and Day of 1967	Hour *	Depth of Haul	Standardized Haul Factor
47 .032	04 01.0N	079 54.0	VIII- 4	0136-N	195	2.77
47 .034	03 11.0N	079 41.0	VIII- 4	0730-D	196	2.77
47 .035	02 57.0N	079 39.0	VIII- 4	1351-D	205	3.13
47 .040	01 41.0N	079 22.0	VIII- 4	2010-N	202	2.69
47 .049	01 00.0N	082 00.0	VIII- 5	1239-D	215	3.67
47 .053	00 18.0N	081 57.0	VIII- 5	2104-N	193	2.91
47 .057	00 22.0S	082 00.0	VIII- 6	0211-N	210	3.38
47 .061	01 11.0S	082 02.0	VIII- 6	0748-D	193	3.09
47 .065	01 46.0S	081 58.0	VIII- 6	1333-D	202	2.48
47 .069	02 27.0S	081 50.0	VIII- 6	2006-N	148	1.94
47 .070	03 06.0S	082 01.0	VIII- 9	2103-N	193	2.53
47 .074	03 58.0S	082 02.0	VIII-10	0305-NT	203	3.35
47 .078	04 39.0S	082 03.0	VIII-10	NOT QUANTITATIVE		
47 .082	05 21.0S	082 02.5	VIII-10	1358-D	204	3.09
47 .086	06 04.0S	082 00.0	VIII-10	1941-N	208	3.06
47 .090	06 47.0S	081 58.0	VIII-11	0211-N	217	3.79
47 .094	07 28.0S	081 56.5	VIII-11	0756-D	218	3.40
47 .097	08 11.0S	082 01.0	VIII-11	1314-D	205	3.20
47 .099	08 48.0S	082 04.0	VIII-11	2111-N	214	3.39
47 .101	09 29.0S	082 05.0	VIII-12	0211-N	220	3.63
47 .103	10 09.0S	082 09.0	VIII-12	0751-D	213	3.51
47 .105	10 02.0S	081 34.0	VIII-12	1246-D	204	3.20
47 .107	09 50.0S	080 53.0	VIII-12	2042-N	196	2.81
47 .109	09 35.0S	080 15.0	VIII-13	0215-N	205	3.23
47 .113	09 22.0S	079 39.0	VIII-13	0733-D	216	3.61
47 .124	12 13.0S	077 39.0	VIII-16	1340-D	200	3.05
47 .128	12 29.0S	078 04.0	VIII-16	2216-N	200	3.00
47 .132	12 44.0S	078 52.0	VIII-17	0304-NT	213	2.50
47 .134	12 56.0S	079 28.0	VIII-17	0746-D	211	3.27
47 .137	13 10.0S	080 13.0	VIII-17	1341-D	210	3.17
47 .139	13 27.0S	081 01.0	VIII-17	1922-N	209	3.24
47 .141	13 38.0S	081 45.0	VIII-18	0107-N	211	3.38
47 .143	13 58.0S	082 25.0	VIII-18	0719-D	213	3.53
47 .145	14 18.0S	083 05.0	VIII-18	1232-D	213	3.47
47 .147	14 33.0S	083 41.0	VIII-18	2121-N	217	3.70
47 .149	14 43.0S	084 21.0	VIII-19	0235-N	214	3.61
47 .151	14 56.0S	085 00.0	VIII-19	0806-D	216	3.75
47 .153	14 17.0S	085 03.0	VIII-19	1259-D	210	3.53
47 .155	13 35.0S	085 00.0	VIII-19	1857-N	214	3.60
47 .157	12 44.0S	085 07.0	VIII-20	0335-NT	209	3.38
47 .159	12 06.5S	084 59.0	VIII-20	0756-D	214	3.82
47 .162	11 30.0S	085 01.3	VIII-20	1349-D	207	3.60
47 .164	10 43.2S	085 04.0	VIII-20	2146-N	215	3.65
47 .166	10 01.0S	085 05.3	VIII-21	0258-NT	211	3.57
47 .168	09 16.8S	085 07.3	VIII-21	0817-D	209	4.06
47 .171	08 35.0S	085 02.3	VIII-21	1325-D	212	3.61
47 .173	07 54.8S	085 06.0	VIII-21	1945-N	216	3.61
47 .175	07 16.0S	085 07.3	VIII-22	0123-N	211	3.80
47 .177	06 35.0S	085 08.5	VIII-22	0754-D	217	2.79
47 .179	05 49.7S	085 00.0	VIII-22	1301-D	221	4.39
47 .181	05 17.0S	085 01.0	VIII-22	2101-N	213	3.85
47 .185	04 28.5S	085 00.0	VIII-23	0309-NT	212	3.82
47 .189	03 51.0S	085 01.0	VIII-23	0837-D	211	3.57
47 .193	02 58.8S	085 01.0	VIII-23	1456-DT	220	4.15
47 .197	02 10.0S	085 03.0	VIII-23	2055-N	222	3.97
47 .201	01 26.0S	085 03.5	VIII-24	0249-NT	209	3.64
47 .205	00 39.5S	085 04.0	VIII-24	0835-D	207	3.61
47 .213	00 47.0N	084 55.0	VIII-24	2141-N	192	3.03
47 .217	01 31.0N	084 55.0	VIII-25	0326-NT	211	3.51
47 .221	02 08.0N	084 57.2	VIII-25	0836-D	211	3.44
47 .225	02 47.0N	084 58.5	VIII-25	1500-DT	200	3.22
47 .229	03 33.0N	084 54.0	VIII-25	2053-N	209	3.63
47 .233	04 21.0N	084 49.0	VIII-26	0248-NT	207	3.26
47 .237	05 06.5N	084 45.0	VIII-26	0835-D	213	3.76
47 .240	05 41.0N	084 56.5	VIII-26	1336-D	205	3.51
47 .242	06 21.0N	084 54.5	VIII-26	1957-N	146	2.10
47 .244	06 59.0N	084 54.0	VIII-27	0156-N	207	3.58
47 .246	07 42.5N	085 04.0	VIII-27	0825-D	204	3.52
47 .250	08 26.5N	085 05.0	VIII-27	1430-D	210	3.61
47 .254	08 56.5N	085 01.0	VIII-27	1946-N	224	4.26
47 .258	09 26.5N	084 52.0	VIII-28	0055-N	213	3.27
47 .268	11 58.0N	088 02.0	VIII-31	0919-D	191	3.30
47 .272	11 20.8N	088 00.0	VIII-31	1441-D	195	3.10
47 .276	10 54.0N	088 10.0	VIII-31	2201-N	183	3.20
47 .278	10 21.0N	088 18.0	IX- 1	0345-DT	219	3.69
47 .280	09 44.5N	088 14.0	IX- 1	0941-D	201	3.46
47 .283	09 04.0N	088 04.0	IX- 1	1512-DT	209	3.80
47 .286	08 15.0N	087 52.0	IX- 1	2117-N	215	3.81
47 .288	07 29.0N	087 44.0	IX- 2	0330-NT	215	3.91
47 .290	06 47.0N	087 57.0	IX- 2	0949-D	207	3.32
47 .292	06 20.0N	087 57.0	IX- 2	1514-DT	207	3.48
47 .295	05 16.0N	087 57.0	IX- 2	2201-N	208	3.53
47 .297	04 38.0N	087 57.0	IX- 3	2246-N	213	3.39
47 .301	04 00.0N	088 02.0	IX- 4	0353-DT	212	3.50
47 .304	03 22.0N	088 04.0	IX- 4	0847-D	211	3.46
47 .306	02 44.8N	087 59.0	IX- 4	1407-D	211	3.52
47 .310	02 02.0N	088 03.0	IX- 4	2027-N	204	3.32
47 .314	01 18.0N	088 06.0	IX- 5	0201-N	220	3.95
47 .318	00 33.5N	088 02.0	IX- 5	0829-D	216	3.90
47 .322	00 13.5S	088 07.0	IX- 5	1446-D	177	2.37
47 .326	00 59.0S	088 06.5	IX- 5	2053-N	150	2.01
47 .330	01 44.5S	088 08.2	IX- 6	0255-NT	185	3.10
47 .334	02 23.5S	088 02.3	IX- 6	0837-D	222	4.51
47 .338	03 04.0S	088 03.5	IX- 6	1421-D	212	4.21
47 .342	03 47.5S	088 03.5	IX- 6	2139-N	215	4.06
47 .345	04 29.0S	087 57.0	IX- 7	0334-NT	209	3.77
47 .349	05 09.5S	088 02.0	IX- 7	0923-D	217	3.95
47 .351	05 53.0S	087 59.0	IX- 7	1513-DT	174	2.60
47 .354	06 36.5S	087 59.0	IX- 7	2057-N	207	3.35
47 .357	07 18.0S	088 01.0	IX- 8	0207-N	205	3.32
47 .359	08 07.0S	088 03.0	IX- 8	0846-D	211	3.65
47 .362	08 55.0S	088 04.0	IX- 8	1421-D	206	3.34
47 .364	09 40.0S	088 02.0	IX- 8	2011-N	163	2.93
47 .367	10 22.0S	088 02.0	IX- 9	0207-N	209	3.23
47 .369	11 02.0S	087 58.0	IX- 9	0756-D	215	3.61
47 .371	11 48.0S	088 00.0	IX- 9	1346-D	205	3.18
47 .373	12 31.0S	088 03.0	IX- 9	2136-N	225	4.02
47 .376	13 13.8S	088 01.0	IX-10	0311-NT	209	3.40
47 .379	13 57.0S	087 57.0	IX-10	0902-D	211	3.69
47 .382	14 47.0S	087 59.0	IX-10	1451-DT	205	3.26

APPENDIX TABLE 8.—Station data: latitude and longitude, date of collection, time of day, depth of haul, and standardized haul factor.—*Continued.*

STATION NUMBER	Latitude	Longitude (W)	Date - Month and Day of 1967	Hour *	Depth of Haul	Standardized Haul Factor
47 .415	11 06.5S	095 01.5	IX-13	0745-D	211	3.14
47 .430	09 27.0S	094 59.0	IX-14	2100-N	209	3.04
47 .432	10 14.7S	095 02.0	IX-15	0253-N	229	3.41
47 .436	08 32.0S	095 01.5	IX-15	1225-D	237	4.51
47 .438	07 39.5S	095 08.5	IX-15	2040-N	214	3.80
47 .440	06 41.0S	095 09.0	IX-16	0258-N	256	4.84
47 .443	05 55.0S	095 08.3	IX-16	0908-D	249	4.26
47 .446	05 01.5S	095 05.5	IX-16	1510-D	173	2.99
47 .450	04 14.0S	095 01.0	IX-16	2036-N	216	4.54
47 .454	03 27.3S	095 00.5	IX-17	0242-N	215	4.08
47 .458	02 40.5S	095 00.5	IX-17	0817-D	161	2.31
47 .462	01 54.0S	095 04.0	IX-17	1356-D	180	2.68
47 .466	01 01.0S	095 08.5	IX-17	2101-N	210	5.19
47 .470	00 24.0S	095 09.2	IX-18	0424-DT	166	1.98
47 .478	01 05.2N	094 57.7	IX-19	1601-DT	205	3.43
47 .486	02 32.5N	094 42.0	IX-19	0313-NT	205	3.00
47 .490	03 16.3N	094 40.8	IX-19	0835-D	222	3.61
47 .494	03 58.0N	094 59.0	IX-19	1349-D	216	3.65
47 .498	04 44.0N	094 55.0	IX-19	2207-N	213	3.51
47 .501	05 36.0N	094 55.5	IX-20	0319-NT	206	3.90
47 .504	06 26.5N	094 58.5	IX-20	0853-D	219	3.39
47 .507	07 19.0N	094 57.5	IX-20	1427-D	209	3.19
47 .509	08 05.0N	095 02.0	IX-20	1955-N	207	2.87
47 .511	08 56.5N	095 04.0	IX-21	0142-N	200	2.83
47 .513	09 49.0N	095 05.0	IX-21	0722-D	193	2.44
47 .515	10 45.5N	095 04.0	IX-21	1321-D	217	3.58
47 .517	11 36.0N	095 00.5	IX-21	2101-N	211	3.48
47 .520	12 33.2N	094 57.0	IX-22	0249-N	205	3.13
47 .523	13 16.0N	095 00.0	IX-22	0748-D	210	3.72
47 .525	14 11.0N	095 01.0	IX-22	1330-D	204	2.92
47 .527	15 00.3N	094 59.0	IX-22	1858-N	204	3.01
CRUISE OP						
OP .001	09 17.4S	079 41.9	XI-14	0228-NT	198	3.00
OP .002	09 41.9S	080 28.4	XI-14	0836-D	255	3.88
OP .003	09 53.6S	080 50.6	XI-14	1231-D	206	3.06
OP .005	10 14.0S	081 26.0	XI-14	1818-N	192	3.41
OP .007	10 40.0S	082 20.5	XI-14	0008-N	191	3.28
OP .009	10 58.4S	082 59.4	XI-15	0626-D	191	2.63
OP .011	11 26.2S	083 51.6	XI-15	1216-D	179	2.87
OP .013	11 58.1S	084 54.6	XI-15	1948-N	205	2.68
OP .015	11 18.9S	084 54.4	XI-15	0001-N	194	3.37
OP .017	10 31.0S	084 54.0	XI-16	NOT QUANTITATIVE		
OP .019	09 40.5S	084 52.8	XI-16	1225-D	214	3.98
OP .021	08 57.1S	084 52.7	XI-16	1827-N	240	4.09
OP .023	07 57.8S	084 53.6	XI-16	0008-N	193	3.38
OP .025	07 13.1S	084 52.7	XI-17	0611-D	205	3.41
OP .027	06 07.8S	084 55.1	XI-17	1153-D	206	3.65
OP .029	05 15.9S	084 53.3	XI-17	1801-N	208	3.32
OP .032	04 12.9S	084 55.8	XI-17	0002-N	216	4.01
OP .036	03 34.3S	084 56.1	XI-18	0601-D	230	4.03
OP .040	02 30.7S	084 57.9	XI-18	1141-D	201	3.44
OP .044	01 57.0S	084 58.0	XI-18	1722-N	218	4.19
OP .048	00 41.1S	084 57.9	XI-18	2331-N	174	2.77
OP .052	00 04.1N	084 57.9	XI-19	0619-D	204	3.60
OP .056	00 17.8S	085 37.8	XI-19	1141-D	223	4.16
OP .060	00 30.6S	086 12.8	XI-19	1753-N	209	3.75
OP .064	00 54.2S	087 09.3	XI-19	2329-N	227	4.29
OP .068	01 10.4S	087 52.2	XI-20	0532-D	216	3.78
OP .072	01 37.8S	088 47.9	XI-20	1123-D	216	3.66
OP .076	01 56.8S	089 26.0	XI-20	1743-N	213	3.87
OP .080	02 20.7S	090 24.7	XI-20	2331-N	226	3.99
OP .084	02 36.6S	091 08.8	XI-21	0518-D	211	4.17
OP .088	02 59.5S	092 02.8	XI-21	1056-D	216	3.00
OP .092	02 11.6S	092 06.1	XI-21	1747-N	211	3.73
OP .096	01 07.5S	092 03.9	XI-21	2329-N	219	3.99
OP .100	00 24.0S	092 05.0	XI-22	0527-D	199	2.89
OP .104	00 46.5N	092 05.8	XI-22	1140-D	214	3.63
OP .108	01 24.8N	092 08.2	XI-22	1730-N	215	4.07
OP .112	02 35.5N	092 03.7	XI-22	2330-N	216	3.96
OP .116	03 15.0N	092 00.3	XI-23	0517-D	205	3.63
OP .120	04 23.6N	091 58.8	XI-23	1139-D	217	3.60
OP .124	05 08.7N	091 56.7	XI-23	1733-N	203	3.50
OP .128	06 08.4N	091 58.9	XI-23	2333-N	203	3.40
OP .132	06 48.3N	092 00.4	XI-24	0515-D	184	2.92
OP .136	07 57.4N	092 02.8	XI-24	1157-D	225	4.03
OP .138	08 12.3N	092 03.2	XI-24	1716-N	193	3.10
OP .155	09 03.1N	092 00.4	XI-25	1153-D	216	3.78
OP .160	10 14.9N	091 59.5	XI-25	2335-N	203	3.51
OP .162	11 09.5N	092 00.3	XI-26	0517-D	181	3.09
OP .164	11 43.5N	091 59.6	XI-26	1242-D	216	4.24
OP .166	12 24.0N	092 01.1	XI-26	1713-N	204	3.40
OP .168	13 21.2N	091 59.4	XI-26	2157-N	212	3.83

DESCRIPTION OF BLACK SEA BASS, *CENTROPRISTIS STRIATA* (LINNAEUS), LARVAE AND THEIR OCCURRENCES NORTH OF CAPE LOOKOUT, NORTH CAROLINA, IN 1966

ARTHUR W. KENDALL, JR.[1]

ABSTRACT

Larvae of black sea bass collected during RV *Dolphin* ichthyoplankton surveys of the mid-Atlantic continental shelf are described. Development of most meristic characters occurs between 6 and 10 mm standard length. The larvae are identified by characteristic ventral pigment patterns, body shape, meristic counts, and lack of extensive armature. The 147 larvae were taken during cruises from June to November 1966, from 4 to 82 km from shore. They were found in tows from the surface to 33 m in water varying in surface temperature from 14.3° to 28.0°C and surface salinity from 30.3 to 34.6‰.

Black sea bass are of considerable economic importance and occur along most of the Atlantic coast of the United States. Although they were first studied in the late 1800's little is reported on their early life history. Spawning is reported to take place in May off North Carolina and in mid-May and June off New Jersey and southern New England (Bigelow and Schroeder, 1953; Miller, 1959). Wilson (1891) described their embryology as part of an incomplete monograph on the species but did not describe the larvae or provide diagnostic characteristics to identify eggs. Hoff (1970) figured a black sea bass egg and prolarva from artificially reared specimens but gave no written description (Figure 1). The eggs are pelagic, clear, round, and 0.9 to 1.0 mm in diameter. They have a smooth shell, narrow perivitelline space, and a single oil globule. They hatch in 75 hr at 16°C and in 38 hr at 23°C (Wilson, 1891; Hoff, 1970). The larvae remain inadequately described although Pearson (1941) identified specimens collected at the mouth of Chesapeake Bay as black sea bass by comparing them with a known series from southern New England using the ventral pigment pattern and fin ray counts. Apparently Merriman and Sclar (1952) had access to the same or similar specimens as Pearson because they pointed out differences between black sea bass and silver hake, *Merluccius bilinearis*, larvae. O. E. Sette's notes, made in connection with his work on Atlantic mackerel, *Scomber scombrus*, early life history contained a mention of black sea bass in a description of bluefish, *Pomatomus saltatrix*, larvae. Larvae of black sea bass have been identified from other collections of ichthyoplankton along the east coast of North America (Perlmutter, 1939; Herman, 1963) with no reference to means of identification. Figures of juveniles, ranging from 39 to 58 mm total length (TL), are shown in Bean (1888), Hildebrand and Schroeder (1928), and Fowler (1945) and reproduced here (Figure 2).

Three species of *Centropristis* occur along the Atlantic coast; *C. striata* is the most widespread and occurs from the Gulf of Maine to the Florida Keys (Miller, 1959). Rock sea bass, *C. philadelphica*, occurs along the Atlantic coast south of Chesapeake Bay, and bank sea bass, *C. ocyurus*, is found generally offshore south of Cape Hatteras. All three species also occur in the Gulf of Mexico, *C. striata* as the subspecies *C. s. melana* (southern sea bass). Black sea bass generally occur over hard bottoms and migrate along the middle Atlantic coast shoreward and northward in summer and offshore and south in

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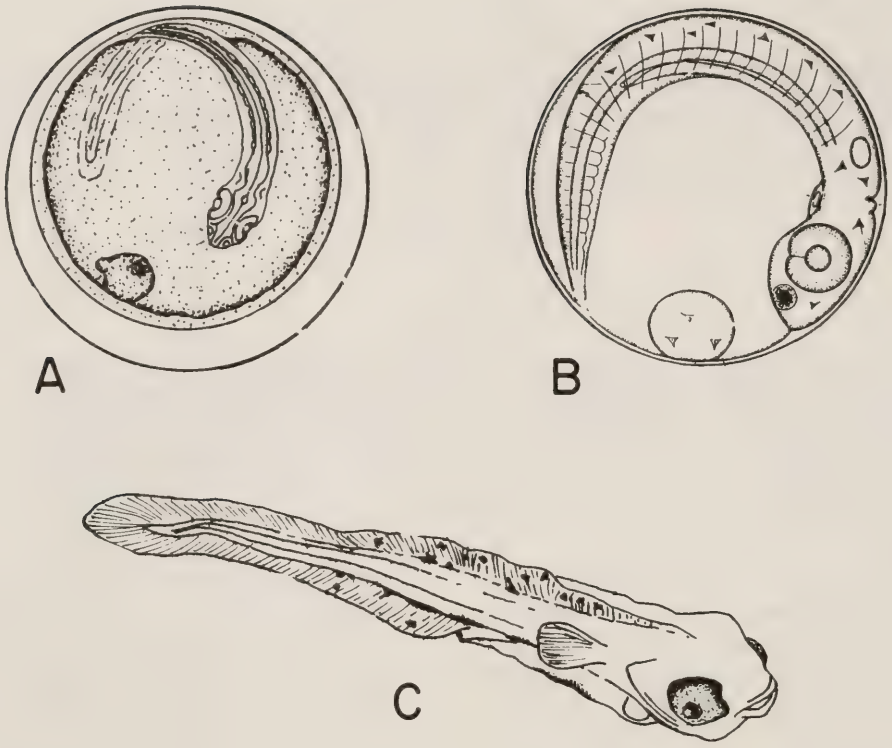

FIGURE 1.—Previously illustrated black sea bass eggs and prolarva. A) egg, 23 hr after fertilization at 23°C, from Hoff (1970, Figure 8); B) egg, 65 hr after fertilization at 16°C, from Wilson (1891, Figure 151); C) prolarva, 54 hr after hatching at 23°C, 2.01 mm TL, from Hoff (1970, Figure 9).

winter. *C. striata* is the only serranid expected to spawn on the continental shelf between Chesapeake Bay and Cape Cod, Mass. (Miller, 1959). Among east coast serranids the unique fin element counts for *Centropristis* for dorsal (X, 11) and anal (III, 7) fins allowed me to determine that I had larvae of this genus. The modal pectoral fin ray count of 18 for black sea bass is distinctive among *Centropristis* and seen on larger larvae. The pigment patterns on larger larvae, whose fin complements were complete, were seen in smaller larvae which appeared to be developing the meristic characters of black sea bass. This was the rationale for identifying the larvae described here as *Centropristis striata*.

On five ichthyoplankton surveys by the RV *Dolphin* between June and November 1966, we collected larval black sea bass at stations between Barnegat Bay, N.J., and Cape Lookout, N.C. This paper describes these larvae and their occurrences.

PROCEDURES

Collecting methods and hydrographic data from the 1965-66 RV *Dolphin* ichthyoplankton survey are reported in detail by Clark et al. (1969). Gulf V plankton tows were taken at 92 stations on eight cruises between Cape Cod, Mass., and Cape Lookout, N.C. The oblique tows covered 4.6 km with one net fishing from the surface to 15 m and, simultaneously, a second, from 18 to 33 m. Samples fixed in 5% buffered

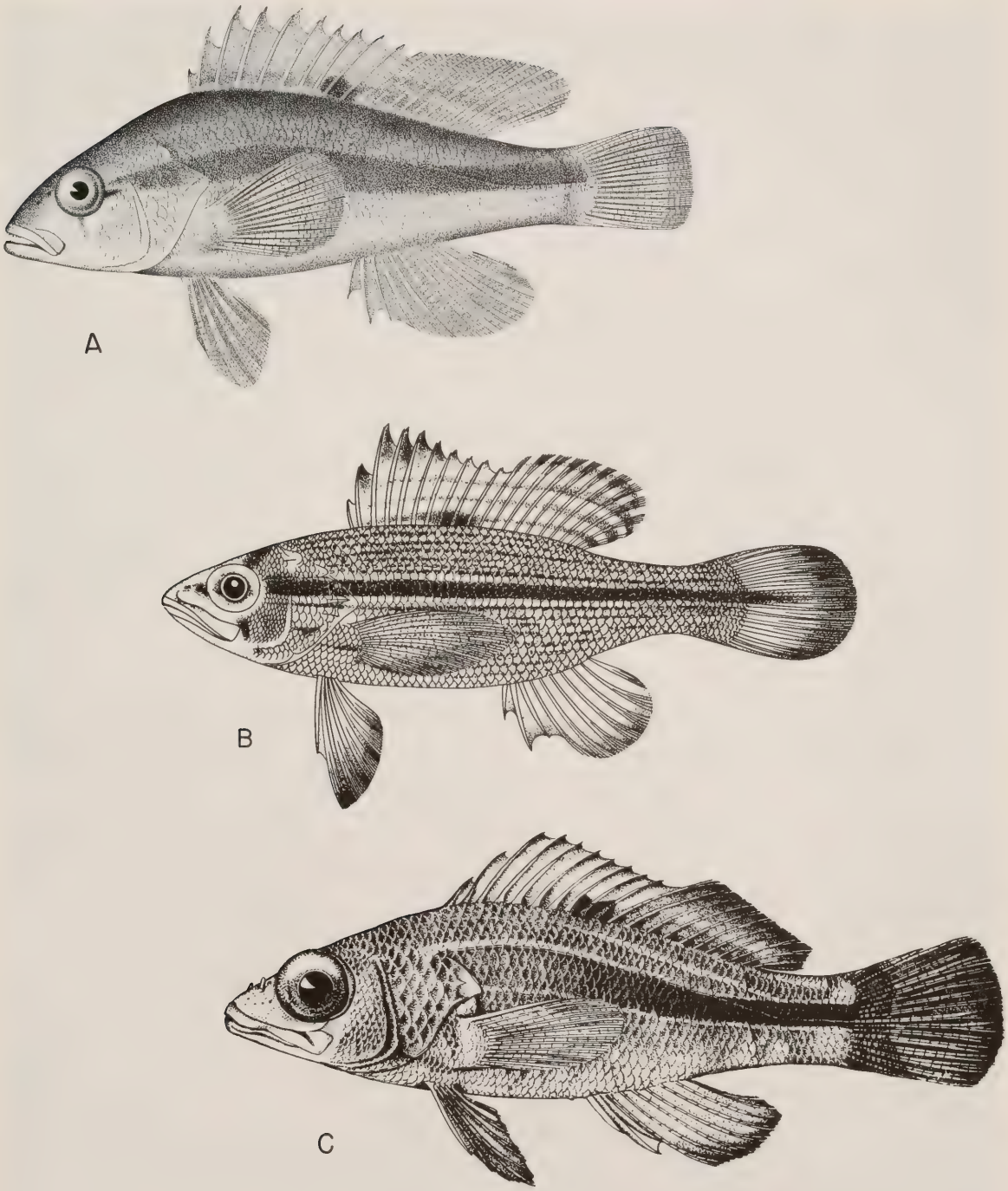

FIGURE 2.—Previously illustrated juvenile black sea bass. A) 39 mm SL, from Bean (1888, Figure 12); B) 42.4 mm SL, from Fowler (1945, Figure 263); C) 58 mm TL (?) from Hildebrand and Schroeder (1928, Figure 144).

Formalin[2] were returned to the laboratory where fish eggs and larvae were removed.

Black sea bass larvae were identified using criteria described, separated from the rest of the larvae in the *Dolphin* collections, counted and measured in standard length (SL). Black sea bass eggs are not well described, and several of their characteristics apply to many other species, so they were not identified in our samples. Other young black sea bass examined included one larva (13.0 mm SL)[3] and several juveniles (37-73 mm SL).[4] Body proportions were measured to the nearest 0.1 mm on selected larvae in Formalin on a depression slide with an ocular micrometer. The base points for larval measurements approximate those used by Ahlstrom and Ball (1954) except body depth, which was measured at the junction of the cleithra, and standard length, measured to the distal ends of the hypurals when formed. Base points for measurements of juveniles follow Hubbs and Lagler (1958). We determined meristic counts on selected specimens lightly stained with alizarin red. Osteological examination was made from specimens cleared and stained following Clothier's (1950) method. Michael P. Fahay illustrated the larvae (Figures 3 and 9).

DESCRIPTION OF LARVAE

In the following description, features useful in identifying black sea bass larvae are emphasized rather than those demonstrating general teleostean development. The approach follows Ahlstrom and Ball (1954) in that each feature is at once traced through its development within the size range (2-13 mm) of the available larvae. Four areas of development are described: armature, body shape, meristic characters, and pigment patterns. Stages of development of black sea bass larvae are illustrated in Figure 3.

[2] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

[3] Collected on October 5, 1967, at Corson Inlet, N.J., by Walter S. Murawski, Jr., New Jersey Department of Conservation and Economic Development.

[4] Inshore seining collections of fish from New Jersey taken by Dr. Albert E. Parr.

ARMATURE

Among larvae of serranids which have been described there is diversity of development of armature. Species of *Epinephelus* develop anterior dorsal and pelvic spines nearly as long as the larva. These spines are barbed and serrated. Preopercular spines are also well developed (Sparta, 1935; Mito, Ukawa, and Higuchi, 1967; Presley, 1970). Larvae of other genera are less ornate and the relative length of fin spines is near that of the adults in some (Bertolini, 1933). Black sea bass larvae are among the serranids with little development of armature. No fin spines are either serrated or pronounced. Pelvic fin spines do not reach the vent; the dorsal and anal fin spines are shorter than the rays. Four to seven short, widely spaced spines are present on the posterior margins of the preopercle and opercle on larvae longer than 5 mm. The three small spines on the opercular flap of the adult form at 8 mm (Figure 3C). Preopercular serrations characteristic of the adult develop early in the juvenile stage.

BODY SHAPE

Changes from larval to adult body form take place over a narrow size range, and the extent of development among fish with similar standard lengths varies. Some body proportions of juvenile and adult black sea bass given by Miller (1959) are compared to those of the developing larvae in this section and in Figures 4 to 6. Between 2 and 5 mm the body proportions remain fairly constant with a slight increase in snout and eye length, and body and caudal peduncle depth, relative to standard length. Most head and body proportions increase significantly between 5 and 6 mm then level off as they approach those of the adult. Caudal peduncle depth and total length, relative to standard length, continue to increase through the larval stage as the caudal fin develops. Body depth, head length, and preanal length proportions increase through the juvenile stage. The adult black sea bass is robust with a large terminal mouth and large head. The back is slightly elevated anteriorly. The dorsal fins are contiguous and the pectorals and pelvics

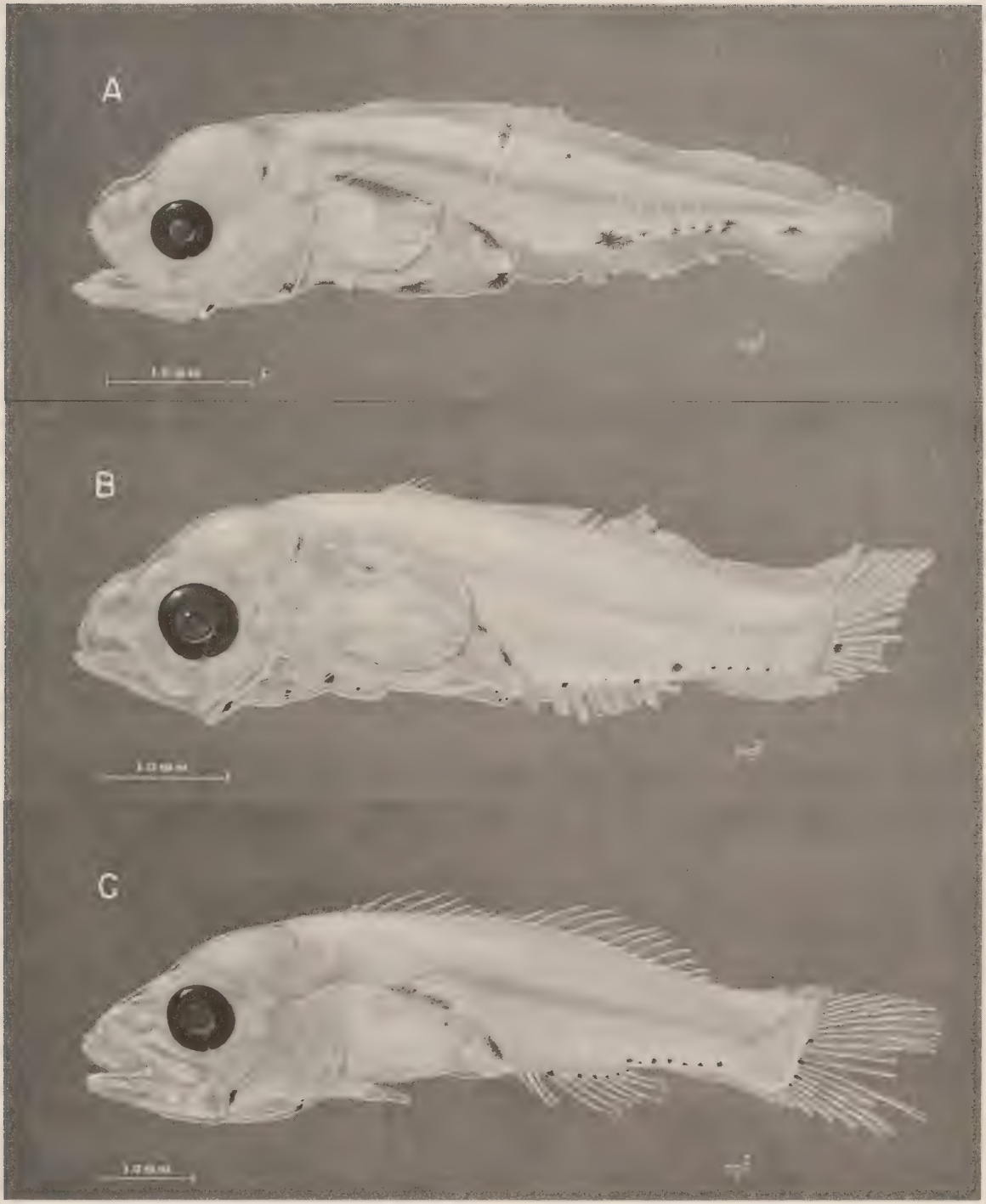

FIGURE 3.—Black sea bass larvae. A) 5.1 mm SL; B) 6.2 mm SL; C) 7.9 mm SL.

are large. The caudal fin outline varies from rounded to trilobed, with one upper ray produced in larger specimens.

Head Length

Between 2 and 4 mm head length averaged about 33% of SL. At 5 mm it reached 37-38% where it remained through 12 mm. Almost all values lie between 30 and 40%, except in a few larvae smaller than 5 mm where precise measurement is difficult. The juveniles demonstrate a continuing trend toward a longer head ranging from 34 to 45% of SL. Miller (1959) gives 40-41% as the proportion in his specimens (Figure 4A).

Eye Length

Eye length remained constant throughout larval development at about 9-10% of SL. Most juveniles as well as Miller's (1959) adult specimens also ranged from 9 to 10% (Figure 4B).

Snout Length

In larvae between 2 and 6 mm snout length increased from 6 to 11% of SL where it holds through adulthood (Miller, 1959) (Figure 4C).

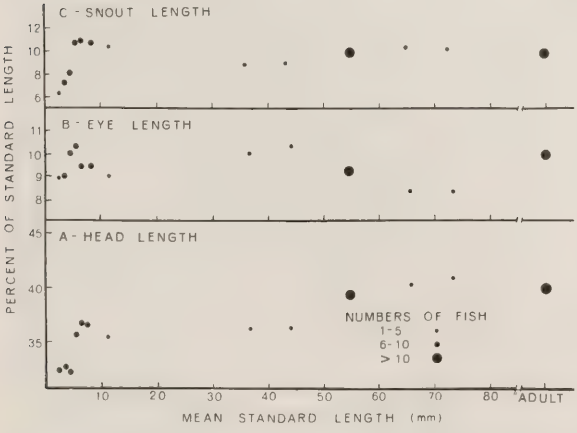

FIGURE 4.—Body proportions of black sea bass associated with the head plotted as percentages of standard length. A) head length; B) eye length; C) snout length. Each point represents the mean of several observations. "Adult" points from Miller (1959).

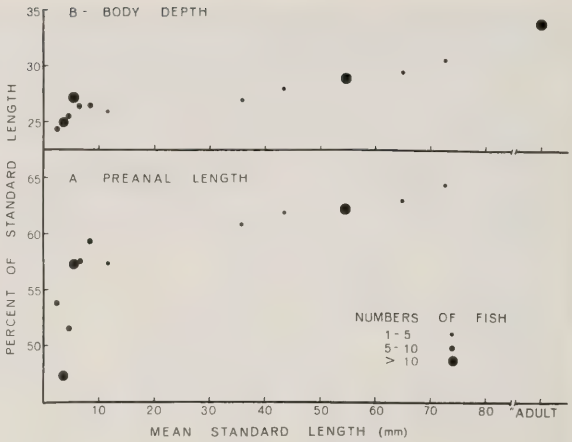

FIGURE 5.—Body proportions of black sea bass associated with the trunk plotted as percentages of standard length. A) preanal length; B) body depth. Each point represents the mean of several observations. "Adult" points from Miller (1959).

Preanal Length

The preanal length increases from about 50% of SL at 5 mm to 58% at 10 mm. During juvenile development it increases to nearly 65% (Figure 5A).

Body Depth

Relative to standard length, body depth increases from about 25 to 27% during larval development. During the juvenile stage it continues to increase to about 30% (Figure 5B). The adult proportion is about 34% (Miller, 1959).

Total Length

Total length is 102% of SL from 2 to 5 mm. As caudal fin development proceeds total length becomes a larger portion of standard length, reaching 120% in our largest larva. It remains constant through juvenile development at about 125% of SL (Figure 6A).

Caudal Peduncle Depth

From 4 mm where caudal peduncle depth is 6% of SL it increases steadily through larval

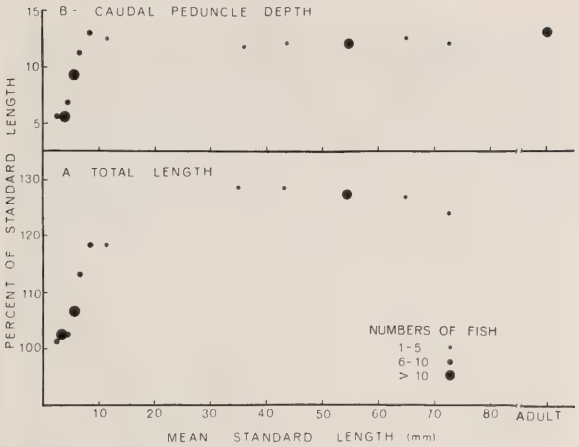

FIGURE 6.—Body proportions of black sea bass associated with caudal fin development plotted as percentages of standard length. A) total length; B) caudal peduncle depth. Each point represents the mean of several observations. "Adult" points from Miller (1959).

development to about 14% where it remains in adults (Miller, 1959) (Figure 6B).

DEVELOPMENT OF MERISTIC CHARACTERS

Most of the meristic features of black sea bass larvae develop within a length range of 4 mm (Table 1). Larvae 5 mm long have undifferentiated finfolds with a few caudal rays, buds of paired fins, some gill rakers and branchiostegal rays, and an incompletely ossified vertebral column (Figure 3A). By 7 mm most median and paired fin elements and branchiostegal rays have formed, some gill rakers are visible, and the vertebral column is ossified (Figure 3B). Other than gill rakers and scales, adult complements of meristic characters are reached by 9 mm (Figure 3C). The following descriptions roughly follow the sequence of attainment of adult characters.

TABLE 1.—Development of meristic characters of larval black sea bass.

SL (mm)	Caudal fin rays				Dorsal fin		Anal fin		Pectoral fin rays	Pectoral fin elements	Vertebrae	Branchiostegal rays	Gill rakers
	Sec.	Primary		Sec.									
	Upper	Upper	Lower	Lower	Spines	Rays	Spines	Rays					
3.2													
3.4													
4.0													
4.1													
4.5												2	
4.5												4	
4.6					1	1					3	7	5
4.8													
4.9											9	4	
5.0											10	4	8
5.0		6	5			1					12	5	6
5.2		6	6						2		14	5	5
5.3		8	6								15	5	5
5.5		6	7								15	5	6
5.5		5	4		5	6		5	3		11	5	5
5.9		6	4			5		5	7		18	3	6
5.9		7	5		7	6		7	5		20	6	8
6.0		8	7		8	8		8	9	3	22	6	8
6.1		5	4		6	9		7	7		22	5	8
6.3		8	7		2	10		8	9	3	16	6	9
6.5		9	7	2	9	8	2	8	12	5	23	7	8
6.6		9	8	1	8	8	2	8	14	4	23	8	8
6.7		9	8	1	14	11	2	8	16	4	24	7	11
6.7		9	8		8	11	2	8	12	4	23	6	7
7.0		9	8	2	9	10	3	7	10	5	24	7	10
7.1		9	8	2	10	10	3	7	14	5	24	7	10
7.7		9	8	3	10	8	3	7	13	6	24	7	11
8.7	4	9	8	4	10	11	3	7	18	6	24	7	10
9.9	4	9	8	3	10	11	3	7	19	6	24	7	11
10.6	9	9	8	8	10	11	3	7	18	6	24	7	14
11.0	9	9	8	8	10	11	3	7	18	6	24	7	16
11.8	5	9	8	5	10	11	3	7	18	6	24	7	15

[1] Damaged.

Teeth

At 5 mm, widely spaced small conical teeth are visible on the premaxillaries (Figure 3A). By 6.5 mm teeth are fairly closely spaced all along the premaxillaries and medially on the dentaries (Figure 3B). By 10 mm the teeth on the premaxillaries are very closely spaced and slightly recurved; those on the dentaries are enlarged and more widely spaced posteriorly but resemble those on the premaxillaries anteriorly.

Axial Skeleton

Ossification of the vertebral column proceeds posteriorly beginning between 4.5 and 5.0 mm. Neural and hemal spines form concurrently with their associated vertebrae. By 5 mm the anterior 12 vertebrae have ossified. By 6.5 mm all of the vertebrae are ossified except two or three anterior to the urostyle. The urostyle ossifies at 6 mm. The penultimate and antepenultimate vertebrae ossify last at 7 mm (Table 1). The first caudal supports to ossify are the medial four hypurals at 6.5 mm. Hypural 1 is ossified at 8.0 mm and hypural 6 is ossified at 8.5 mm. The uroneural and epurals form at 10 mm.

The structure of the caudal region at 11.8 mm (Figure 7) varies only slightly from the typical perciform type described by Gosline (1961). As in other serranids, the two separate uroneurals have fused, but no fusion of the hypurals has occurred. Otherwise the caudal skeleton is typical, having three epurals, a urostyle with a single ossification, and the hemal arch on the antepenultimate and penultimate vertebrae being autogenous (not fused to the vertebrae). There are 15 branched segmented rays supported by six hypurals, 7 ventrally on hypurals 1, 2, and 3 and 8 dorsally on hypurals 4, 5, and 6. One ray dorsal and one ray ventral to these are also segmented but not branched. About eight raylets form dorsally and an equal number form ventrally anterior to the segmented rays. If the first hypural is considered a parhypural (Nybelin, 1963), black sea bass have only two ventral hypurals.

Branchiostegal Rays

The first branchiostegal rays form at about 4.5 mm. By 5 mm four to six rays have formed and at 6.5 mm the adult complement of seven rays is reached, with the medial ones being the last to form (Table 1).

Caudal Fin

From 2 to 4 mm the finfold is symmetrical around the tip of the notochord. Actinotrichs are formed adjacent to the posterior 10% of the

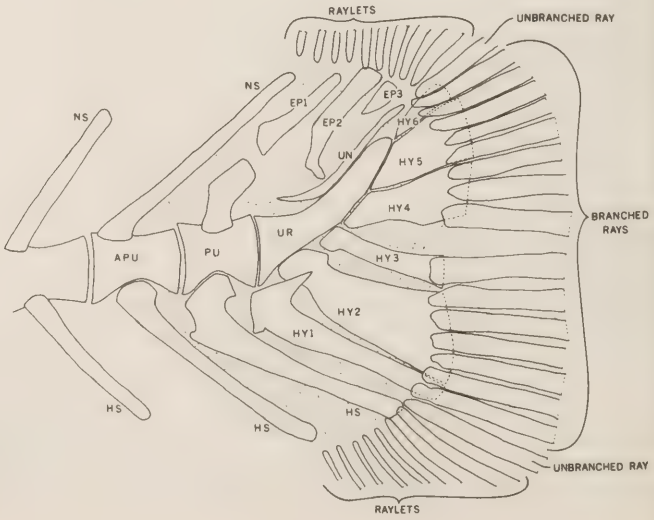

FIGURE 7.—Caudal skeleton of a black sea bass larva 11.8 mm SL. APU = antepenultimate vertebra; EP = epural; HS = hemal spine; HY = hypural; NS = neural spine; PU = penultimate vertebra; UN = uroneural; UR = urostyle.

notochord. Between 4 and 5 mm the anlage of the base of the caudal fin starts to form ventral to the notochord, just anterior to its tip (Figure 3A). By 5.5 mm the notochord is slightly upturned, the developing hypural region appears bilobed and about nine primary caudal rays are formed. The caudal fin at 6 mm has a rounded homocercal outline and eight segmented principal rays in the superior lobe and seven in the inferior lobe (Figure 3B); the rays are branched and some secondary procurrent rays are present. At 8 mm the dorsal hypurals are slightly longer than the ventral ones and the rays and raylets are more clearly defined and approaching the adult complement (Table 1).

Anal Fin

Between 2 and 5 mm there is an undifferentiated finfold in the area of the anal fin. Between 5 and 6 mm, fin rays start to form in the anal finfold between the vent and the most prominent pigment spot on the ventral surface of the trunk (Figure 3A). By 6 mm about six rays and one anal spine are seen (Figure 3B). The finfold posterior to the fin is reduced. By 7 mm the three anal spines are formed. The second spine is first to form and is most prominent throughout development (Figure 3C). The third spine forms as a ray; by 7 mm the spinous form is apparent. The first spine is smaller than the others and forms last at 6.5 mm. By 7 mm the adult complement of seven anal rays is reached and some are branched (Table 1).

Dorsal Fins

The undifferentiated dorsal finfold extends from the nape to the caudal region at 4 mm. By 5 mm the finfold becomes elevated about halfway back on the body where fin ray development begins (Figure 3A). Rays and spines develop along the dorsal fin base and the dorsal finfold posterior to the dorsal fin disappears between 5.5 and 6.5 mm. The anterior spines and posterior rays develop at a smaller size than intermediate fin elements.

The first four dorsal spines are visible by 6 mm. The second through fourth are longer and remain so. The first dorsal spine is about half as long as the second. The second and third spines are the same length at 6.5 but, by 10 mm, the third has become 1.5 times longer than the second. The fourth spine, the longest, is slightly longer than the third. The final complement of 10 spines and 11 rays is attained by 8.7 mm (Table 1). The rays are branched and segmented by 8 mm (Figure 3C).

Median Fin Supports

Anterior interneurals and the interhemal supporting the second anal spine ossify concurrently at about 8.5 mm. By 10 mm most of the interneurals and interhemals are formed. The anterior two interneurals fuse to support the first two dorsal spines (Figure 8). The first two anal spines are supported by one interhemal, apparently formed by fusion of two elements (Figure 8).

Pelvic Fins

Buds of the pelvic fins are seen on 4-mm larvae. Fin rays form between 4 and 6 mm. Rays and spines are first seen between 5 and 6 mm (Figure 3B). At 8 mm the adult complement of one spine and five rays has formed, with the smooth spine two-thirds as long as the longest ray (Table 1).

Pectoral Fins

Pectoral fin buds are present on the smallest larvae (2.1 mm) examined. The early pectorals change little until fin rays appear between 5 and 6 mm. By 6.5 mm the rays are mostly formed and the adult complement of 18 or 19 rays is reached by 9 mm (Table 1).

Gill Rakers

At 5 mm gill rakers appear as a few tubercles on the gill arches. By 6 mm there are nine rakers on the lower limb and none on the upper. At 10.6 mm there are 4 rakers on the upper and 10 on the lower limb. The adult complement of about 10 upper and 18 lower is reached in juveniles.

Scales

Scale formation occurs at a size between the largest larva (13.0 mm), which is scaleless, and the smallest juvenile (37 mm) in our collections.

PIGMENT PATTERNS

Pigmentation on Formalin-preserved black sea bass consists of a few melanophores in characteristic positions, mainly along the ventral part of the larva (Figure 9). Other kinds of larvae in the collections with spots in similar positions had meristic counts and body shapes approximating black sea bass. However, the relative size of the various spots in combination with examination of the sequence of development of meristic characters, the distinctive fin element counts on larger larvae, and body shape assured separation of black sea bass from other larvae.

Head Region

At 5 mm one spot usually forms ventrally on the median cartilage between the dentaries and urohyal. A second forms posterior to this on some specimens (Figure 9). A spot forms at 4 mm on each angular (Figure 3A). A characteristic transverse dentritic spot forms immediately anterior to the symphysis of the cleithra. Usually there is a spot between the bases of the pelvic fins. Dorsally there is a variable number of spots irregularly spaced on the posterodorsal covering of the cerebellum, and generally a pair of spots internally on the posterior surface of the midbrain. Between 12 and 13 mm a band of minute melanophores develops from the angular, past the eye, to the anterior part of the cerebellum. There are also several larger spots on the anterior halves of the cerebral hemispheres and a group of spots which originate at the eye and extend posteriorly to the opercular flap.

Gut Region

Considerable internal pigmentation develops in the dorsal area of the gut cavity, mostly on the surface of the viscera. These are large spots but superficially not readily definable. In larvae up to about 6 mm, this pigment reaches the exterior as a large intense spot on the posterior region of the renal tract (Figures 3A and B). In some specimens there is a smaller spot just anterior to the vent and another one about midway between the origin of the pelvic fins and the vent, along the midventral line (Figure 9).

Trunk and Caudal Region

Occasionally a few irregular spots occur dorsally on the trunk about midway on the body. Between 12 and 13 mm, a series of about six groups

FIGURE 8.—Cleared and stained black sea bass larva 11.8 mm SL.

FIGURE 9.—Ventral view of pigment on a 5.4-mm black sea bass larva.

of small melanophores develops along the lateral line. At this length a few spots also develop at the origin of the dorsal fin. As the anal fin rays form, spots develop at some of their bases. A prominent spot forms early, near the posterior end of the anal fin; it is followed by four to six smaller spots along the midventral line that extends to the base of the caudal fin where there is another large spot. Before notochord flexion there is a prominent spot on the developing fin rays (Figure 9). This persists as the fin develops and reaches a position at the bases of some of the ventral rays of the caudal fin. As the caudal rays develop, some less prominent spots appear on rays dorsally and ventrally from the first spot. The pigment in the caudal region and along the midventral line persists through larval development.

LARVAL OCCURRENCES

Black sea bass larvae were taken on five cruises from June to November 1966, between Sandy Hook, N.J., and Cape Lookout, N.C. (Appendix Table). Of 39 tows containing black sea bass larvae, 20 had only one larva, and only two had more than 20 larvae; thus only limited inference about their distribution and relative abundance can be derived from these data. Larvae were taken in both shallow (0-15 m) and deep (18-33 m) tows from 4 to 82 km from shore. Water depths in the areas of capture ranged from 15 to 51 m. Surface temperature varied from 14.3° to 28.0°C; that on the bottom from 8.3° to 26.6°C. Surface salinity varied from 30.3 to 34.6‰.

Seasonally, there seems to be some northerly progression of spawning. During June one larva was taken off Oregon Inlet, N.C., and one off Paramore Island, Va. (Figure 10). During August, larvae occurred from Cape Henlopen, Del., to Ocracoke Inlet, N.C., being most abundant off Maryland and Virginia (Figure 11).

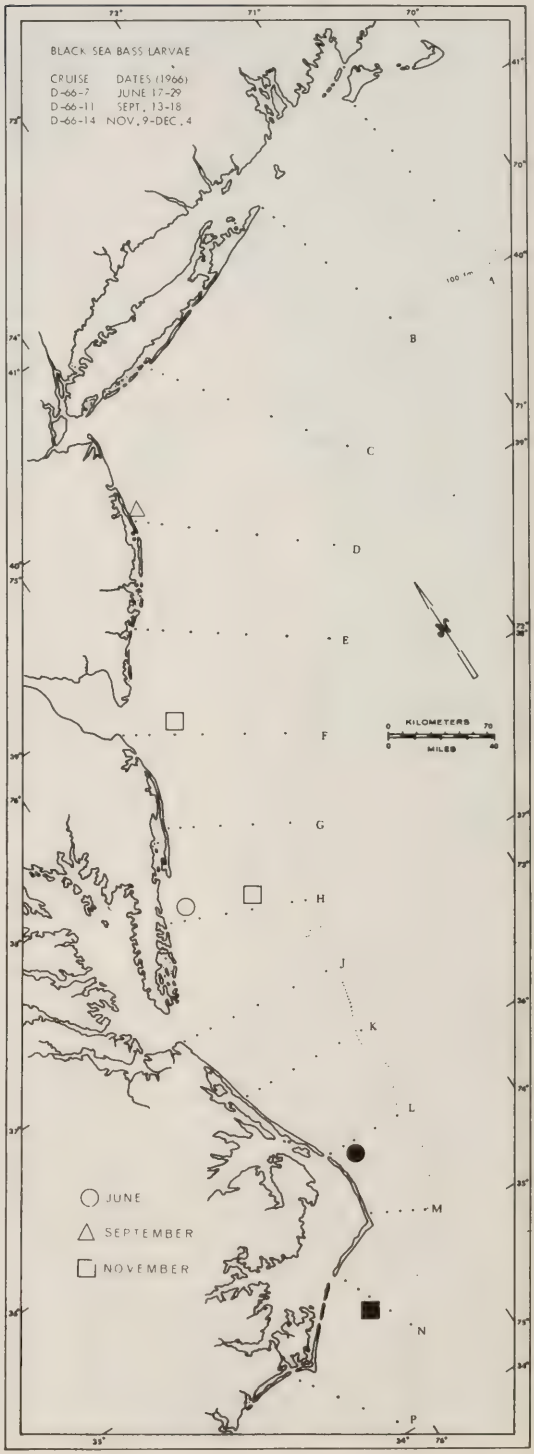

FIGURE 10.—Occurrence of black sea bass larvae in shallow (0-15 m) (open symbols) and deep (18-33 m) (solid symbols) tows. Three RV *Dolphin* cruises, 1966.

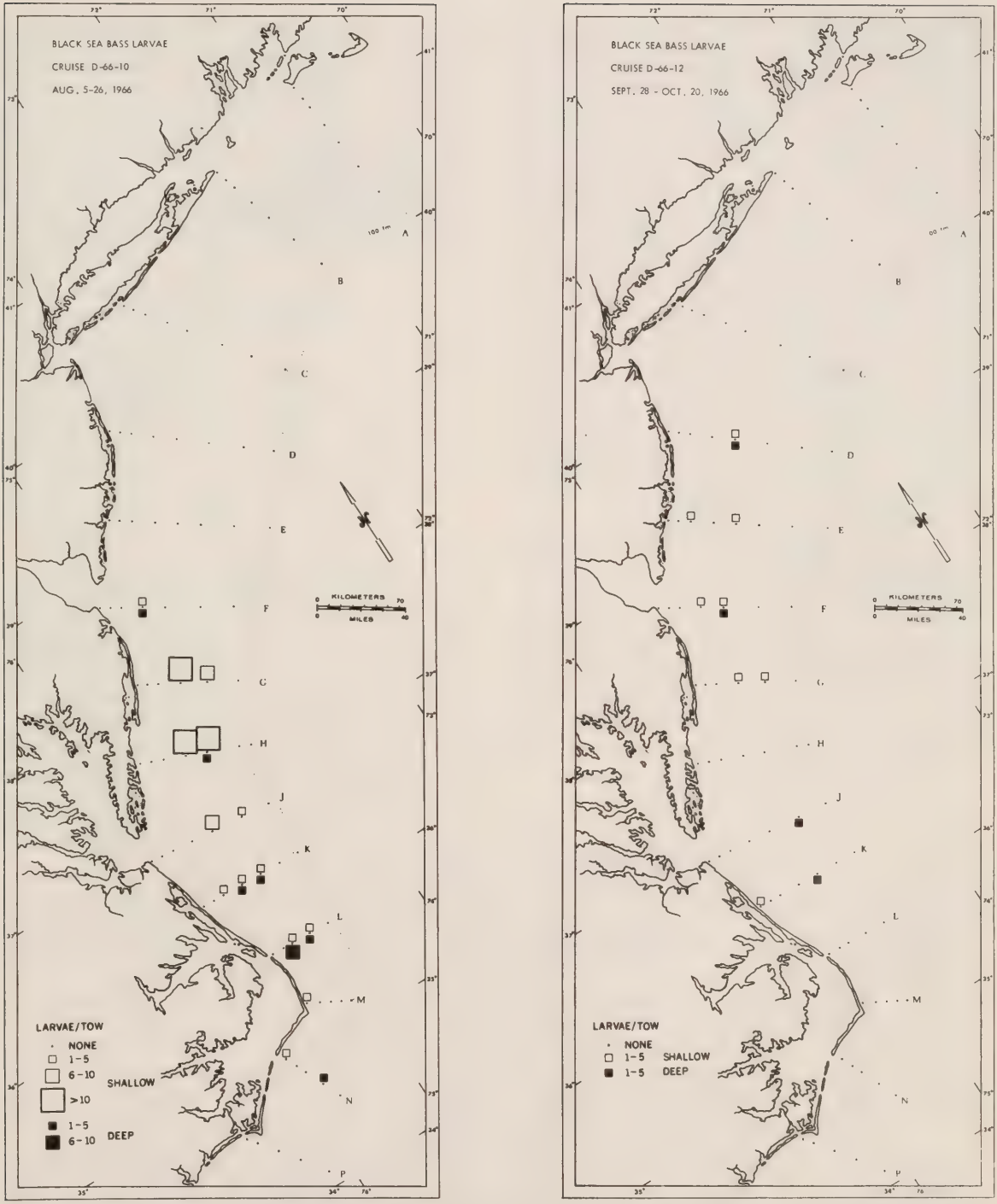

FIGURE 11.—Distribution and abundance of black sea bass larvae in August (left) and October (right) from RV *Dolphin* cruises.

During September only the four northern transects were sampled and the only larva taken was off Barnegat Inlet, N.J. (Figure 10). During October larvae ranged from Great Egg Inlet, N.J., to Currituck Light, N.C. In November four larvae occurred between Cape Henlopen, Del., and Ocracoke Inlet, N.C. (Figure 10).

The larvae ranged from 2.1 to 13.0 mm SL (Figure 12). Among the cruises the mean size of larvae was nearly constant. The length-frequency curve indicates that we undersampled small larvae (< 4 mm), probably because they were extruded through the meshes of the net. Comparisons of mean lengths of larvae taken during day and night and in shallow and deep tows for the individual cruises were made. Larvae in the deep net were slightly larger than those in the shallow net. Day-night differences in size were inconclusive (Table 2). Geographic variations in size are not apparent.

A comparison of fish caught per successful tow in shallow and deep tows taken during day and night shows that more fish were taken in shallow than in deep tows and more were taken at night than during day (Table 2). Our data on size and diurnal and depth distribution of the larvae indicate several things. More and slightly larger larvae were taken at night than during the day. Also, larvae in the deep net were slightly larger than those in the shallow net. More larvae were taken in the shallow than in the deep net. Thus it appears that larvae are more abundant near the surface (0-15 m) than deeper (18-33 m) waters and that visual warning allows larger larvae to escape in near surface waters, particularly during the day.

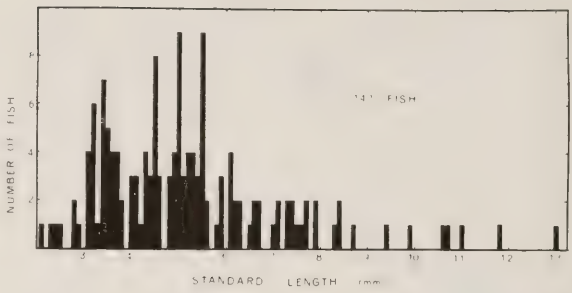

FIGURE 12.—Length distribution of black sea bass larvae from RV *Dolphin* cruises, 1966.

DISCUSSION

The general distribution of larvae and juveniles of black sea bass can be deduced from their occurrence in several disjunct studies of estuaries and coastal waters of the Atlantic coast. Early larvae (< 6 mm) have been found at the mouth of Chesapeake Bay (Pearson, 1941), in Long Island Sound (Perlmutter, 1939), and in Narragansett Bay (Herman, 1963). The lack of black sea bass larvae in some intensive sur-

TABLE 2.—Black sea bass larvae from 1966 RV *Dolphin* cruises. Total numbers, numbers per positive tow, and lengths in shallow and deep tows by cruise and time of day.

Cruise	Time of day	Shallow				Deep			
				Length (mm)				Length (mm)	
		No.	No./tow	Range	Mean	No.	No./tow	Range	Mean
June	Day	1	1.0	4.6	4.6				
	Night					2	2.0	5.5- 5.9	5.7
Aug.	Day	32	6.4	2.1- 5.5	3.7	2	1.0	5.4- 7.9	6.7
	Night	72	9.0	2.8-10.7	5.4	16	3.2	2.5-11.8	6.3
Sept.	Day	1	1.0	5.4	5.4				
	Night								
Oct.	Day	7	1.8	4.3- 6.3	5.5				
	Night	6	1.5	3.5- 6.1	5.1	4	1.0	3.6- 7.3	5.5
Nov.	Day	1	1.0	7.5	7.5	2	2.0	7.6-13.0	10.3
	Night	1	1.0	5.2	5.2				
Day total or mean		42	3.5	2.1- 7.5	4.2	4	1.3	5.4-13.0	6.8
Night total or mean		79	6.1	2.8-10.7	5.4	22	2.2	2.5-11.8	6.1
Grand total or mean		121	4.8	2.1-10.7	5.0	26	2.0	2.5-13.0	6.5

veys along the Atlantic coast is remarkable (e.g., Merriman and Sclar, 1952; Wheatland, 1956; Richards, 1959; Massmann, Joseph, and Norcross, 1962; Marak et al., 1962). Ichthyoplankton sampling in more enclosed areas, such as Indian River, Del. (Pacheco and Grant, 1965) and Sandy Hook Bay, N.J. (Croker, 1965), has failed to reveal larvae. Juveniles (25-75 mm) have been taken from saline areas of estuaries from Florida (Tagatz, 1968), Maryland (Schwartz, 1961, 1964), Delaware (de Sylva, Kalber, and Shuster, 1962), New York (Perlmutter, 1939; Greeley, 1939; Richards, 1963), Rhode Island (Herman, 1963), and Massachusetts (Lux and Nichy, 1971). Bean (1888) reported that young about 1 inch (25 mm) long were common in Great Egg Harbor Bay, N.J., and Nichols and Breder (1927) reported 20-mm fish over oyster beds off Staten Island, N.Y., in August. Massmann et al. (1962) found one 43-mm juvenile in the ocean off Virginia.

Black sea bass spawn offshore along the coast from Florida to New England. Spawning takes place earlier in the southern part of the range than in the northern part; in May off North Carolina (Smith, 1907); in late May off Chesapeake Bay (Hildebrand and Schroeder, 1928); and into early summer off southern New England (Bigelow and Schroeder, 1953). At least some of the young, less than 30 mm, enter open estuaries near inlets where they spend their first summer associated with hard bottoms such as oyster shells (Nichols and Breder, 1927; Arve, 1960; Richards, 1963). Young leave the estuaries during fall and return during spring. Enough return to estuaries in subsequent years to support fisheries there. From references made to black sea bass abundance around the turn of the century (Bean, 1888; Smith, 1898; Sherwood and Edwards, 1901), it seems that present stocks in the northern part of the range are diminished. This decrease in abundance may be associated with decrease in oyster beds (Arve, 1960). Commercial catch records show recent catches near the historical mean, but indicate a shift in abundance from the New York-Delaware to the Chesapeake region (Lyles, 1967).

Our data on offshore occurrences of larvae complement work in estuaries where early stages have been found. However, a definitive picture of the early life history of this species is still lacking. The small numbers of larvae taken in this survey do not seem consistent with the population size and extent of adult black sea bass along the coast. Possibly we sampled in a year when spawning was unsuccessful or our sampling was not effective for capturing black sea bass larvae in proportion to their abundance.

The pelagic existence of this fish is short. Larvae longer than 13 mm were not taken, presumably because near that size they assume demersal or estuarine habits. Few of these late larvae and early juveniles have been collected, and it is still not known what part of the population may enter estuarine waters and what part remains at sea. The routes and mechanisms of larval transport from spawning grounds to nursery areas are also unknown.

The known seasonal distribution of larvae shows that black sea bass spawn over a long period. The range of juvenile sizes taken in individual samples also indicates a long spawning season. Details of the suggested northward progression of spawning need clarification. Intensive sampling of the water column and bottom offshore, at inlets, and in open estuaries could resolve these deficiencies in our knowledge of black sea bass life history.

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APPENDIX TABLE.—RV *Dolphin* 1965-66 ichthyoplankton survey. Data associated with Gulf V catches of black sea bass larvae.

Cruise station	Tow depth (m)	Larvae			Date (1966)		Tow start time (EST)	Light condition[1]	Water depth (m)	Temperature (°C)				Thermocline		Salinity (‰)	
		Number	Lengths (mm SL)		D	M				Range	Mean	Surface	Bottom	Degree	Depth (m)	Range	Mean
			Mean	Range													
D-66-7																	
H 2	0- 6	1	4.6		27	6	1521	Day	22	18.1-21.2	19.6	21.2	15.5	Weak	2-11	30.3-31.0	30.7
L 3	18-24	2	5.7	5.5- 5.9	22	6	2144	Night	38	15.3-15.4	15.3	16.7	15.6	None	--	32.8-32.8	32.8
D-66-10																	
F 5	0-15	3	3.6	2.8- 4.5	9	8	2352	Night	34	14.8-22.4	20.7	22.4	8.6	Strong	9-19	30.9-30.9	30.9
F 5	18-24	1	3.7		9	8	2352	Night	34	8.8-11.5	9.5	22.4	8.6	Strong	9-19	31.1-31.3	31.2
G 4	0-15	17	3.6	2.3- 5.1	21	8	0930	Day	28	15.8-23.6	21.9	23.6	9.7	Strong	8-18	30.7-31.0	30.9
G 5	0-15	7	4.0	3.1- 5.5	21	8	1255	Day	49	16.3-24.2	21.2	24.2	5.8	Strong	3-23	30.1-30.8	30.4
H 4	0-15	24	5.9	3.2-10.6	22	8	0305	Night	26	12.6-24.5	21.6	24.5	9.8	Strong	10-17	30.5-31.1	30.6
H 5	0-15	28	4.9	3.2- 7.3	22	8	0139	Night	40	18.8-25.4	23.7	25.4	8.4	Strong	11-22	30.5-31.0	30.7
H 5	18-24	3	5.3	4.8- 6.1	22	8	0139	Night	40	9.7-14.8	11.7	25.4	8.4	Strong	11-22	31.0-31.2	31.1
J 5	0-15	8	6.5	4.2-10.7	22	8	2347	Night	26	15.7-26.1	21.2	26.1	10.3	None	--	30.4-31.2	30.7
J 6	0-15	1	9.4		23	8	0335	Night	35	18.5-25.8	23.6	25.7	8.3	Strong	6-24	30.3-30.6	30.5
K 3	0-15	2	4.6	3.2- 6.1	24	8	1954	Night	25	15.0-24.4	22.1	24.4	14.8	Strong	7-15	30.7-31.1	30.8
K 4	0-15	21			23	8	1857	Night	27	14.5-25.5	22.0	25.5	10.5	Strong	8-18	30.3-31.3	30.9
K 4	18-24	2	11.4	11.0-11.8	23	8	1857	Night	27	10.8-12.9	11.7	25.5	10.5	Strong	8-18	30.8-31.6	31.3
K 5	0-15	2	5.0	5.0- 5.0	23	8	1718	Day	30	19.4-26.4	22.9	26.4	9.6	Strong	7-23	31.2-31.3	31.3
K 5	18-24	1	5.4		23	8	1718	Day	30	10.2-15.4	12.3	26.4	9.6	Strong	7-23	31.4-31.7	31.6
L 3	0-15	5	4.5	3.2- 6.3	25	8	0445	Night	33	16.9-24.6	22.2	24.6	16.4	Strong	7-14	31.3-31.9	31.5
L 3	18-24	8	6.6	3.6- 8.4	25	8	0445	Night	33	14.7-16.4	15.6	24.6	16.4	Strong	7-14	32.2-32.7	32.5
L 4	0-15	5	3.2	2.1- 4.3	25	8	0618	Day	41	24.9-25.8	25.6	25.8	16.0	Strong	19-25	31.9-33.6	32.4
L 4	18-33	1	7.9	7.9- 7.9	25	8	0618	Day	41	15.6-24.1	18.1	25.8	16.0	Strong	19-25	31.2-34.5	33.3
M 1	0- 6	1	3.3		25	8	1212	Day	15	25.4-25.4	25.4	25.4	25.4	None	--	31.4-31.6	31.5
N 1	0-15	1	4.5		25	8	2036	Night	22	27.1-27.2	27.2	27.2	26.6	None	--	34.6-34.8	34.7
N 4	18-33	2	2.7	2.5- 2.9	26	8	0009	Night	48	22.9-27.5	25.2	28.0	21.6	Weak	17-41	34.8-35.3	35.0
D-66-11																	
D 1	0- 6	1	5.4		18	9	1413	Day	16	21.0-21.1	21.0	21.1	20.7	None	--	30.4-30.5	30.5
D-66-12																	
D 5	0-15	1	5.0		12	10	2204	Night	36	16.5-16.6	16.6	16.6	11.0	Weak	23-37	31.2-31.3	31.2
D 5	18-24	1	7.1		12	10	2204	Night	36	15.5-16.4	16.1	16.6	11.0	Weak	23-37	31.2-31.4	31.3
E 3	0- 6	1	5.0		5	10	1323	Day	22	17.4-17.4	17.4	17.4	16.9	None	--	30.8-30.9	30.8
E 5	0-15	11	6.1		11	10	2210	Night	35	16.4-16.6	16.5	16.6	9.0	Strong	22-31	31.2-31.4	31.3
F 4	0-15	2	4.2	3.5- 5.0	5	10	0227	Night	22	17.7-18.0	17.8	18.0	17.7	None	--	30.8-30.9	30.8
F 5	0-15	2	5.4	5.3- 5.6	4	10	2151	Night	35	17.4-17.9	17.7	17.9	14.2	Weak	18-24	30.7-30.9	30.8
F 5	18-24	1	3.6		4	10	2151	Night	35	14.9-17.0	16.1	17.9	14.2	Weak	18-24	30.9-30.9	30.9
G 4	0-15	1	6.3		4	10	0627	Day	31	18.1-18.2	18.2	18.2	15.8	None	--	31.0-31.1	31.0
G 5	0-15	4	5.8	5.5- 6.1	4	10	0816	Day	51	17.4-18.0	17.8	18.0	9.4	Strong	19-26	30.9-31.0	30.9
J 6	18-24	1	4.1		2	10	2125	Night	35	14.9-18.0	16.6	19.5	10.1	Weak	16-28	31.5-31.6	31.5
K 1	0-15	1	4.3		1	10	0730	Day	17	19.7-21.4	20.8	21.4	19.7	None	--	30.4-30.9	30.6
K 5	18-24	1	7.3		1	10	0010	Night	33	12.9-15.9	13.9	21.6	12.3	Weak	11-22	30.8-31.0	30.9
D-66-14																	
F 4	0-15	1	5.2		11	11	0312	Night	22	14.2-14.3	14.2	14.3	14.2	None	--	32.8-33.0	32.9
H 5	0-15	1	7.5		12	11	0754	Day	42	14.4-15.3	14.8	15.3	14.0	None	--	33.3-33.6	33.5
N 3	18-24	2	10.3	7.6-13.0	16	11	0833	Day	30	19.4-19.5	19.4	19.3	19.4	None	--	35.8-35.9	35.9

[1] Day tow: start time between sunrise and 0.5 hr before sunset; night tow: start time between sunset and 0.5 hr before sunrise.
[2] Larva too mutilated for accurate measurement.

UREA AND OTHER NITROGENOUS NUTRIENTS IN LA JOLLA BAY DURING FEBRUARY, MARCH, AND APRIL 1970

JAMES J. MCCARTHY[1] AND DANIEL KAMYKOWSKI[2]

ABSTRACT

Samples collected from La Jolla Bay twice weekly for 2½ months were analyzed for nitrate, nitrite, ammonium, and urea in addition to other chemical, physical, and biological parameters. On the basis of an infestation of blue sharks (*Prionace glauca*), periods before, during, and after the infestation were defined. Statistical analyses indicated that: 1) Urea concentrations were highest during the period of shark infestation. 2) There was strong positive correlation between phaeo-pigment/chlorophyll ratios and ammonium concentrations during the infestation but none between the pigment ratios and either the ammonium concentrations for the other two periods or the urea concentrations for any of the three periods. 3) There was no correlation between ammonium and urea concentrations before, a strong positive correlation during, and no correlation after the shark infestation. 4) Urea was the only nitrogenous nutrient for which the concentrations above and below the thermocline were not different. 5) Comparisons between two stations 1.5 km distant indicate that on a horizontal scale, the patch structure for urea is smaller than that of the other nitrogenous nutrients although the median urea concentration in the water column was not different at the two stations.

The temporal similarity and the more complex patch structure for urea (as seen in 4 and 5 above) suggest that the blue sharks were responsible for the higher urea concentrations during the infestation. Although the median ammonium concentrations before and during the infestation were not different, the strong positive correlation between ammonium and urea concentrations during the infestation hint that the sources or rates of supply and utilization for both nutrients may have been closely related. The strong positive correlation between phaeo-pigment/chlorophyll ratios and ammonium concentrations during the infestation may imply that the source of ammonium was herbivore excretion.

The nitrogenous plant nutrients in the marine environment classically include the nitrate, nitrite, and ammonium ions. The fixation of dissolved gaseous nitrogen has been observed in both the Sargasso Sea and Arabian Sea (Dugdale, Goering, and Ryther, 1964) and may for certain areas be a significant process (Dugdale and Goering, 1967). More recently, evidence has been presented which suggests that both urea (McCarthy, 1971) and certain amino acids (North and Stephens, 1971) may also be of importance as nitrogenous nutrients. The purpose of the present study was to compare the pattern of distribution for urea with those for ammonium, nitrite, nitrate, and other chemical, physical, and biological parameters in the La Jolla coastal waters.

In contrast to the other nitrogenous nutrients, little is known about the distribution, the importance, or the cycle of either urea or amino acids in marine waters. The results of quantitative analyses for urea in a total of approximately 120 samples of seawater have been reported by Newell (1967) and McCarthy (1970). Newell's samples were collected from a depth of 10 m at 25 stations in the English Channel and 45 of

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McCarthy's were collected from 9 profiles (5 samples each) in the euphotic zone of the Peru Current. One of the obvious features of both sets of data is the high degree of variability between samples, even those only a few meters vertically distant from one another. There was no consistent pattern in the profile data although higher values tended to occur at intermediate depths in the euphotic zone. It has been shown that urea accounts for a significant fraction of phytoplankton nitrogen uptake off the coast of southern California (McCarthy, in press), and it has been suggested that animal excretion is the major source of urea in the euphotic zone of that area (McCarthy and Whitledge, 1972).

Ammonium concentrations are usually low in coastal waters, but this ion can, at times, be the most abundant form of nitrogen available for phytoplankton utilization. It is the major nitrogenous excretory product of most marine animals (Parry, 1960; Baldwin, 1964) and as such is recycled rapidly in surface waters. The importance of ammonium in phytoplankton nutrition has been demonstrated in the eastern tropical Pacific by Thomas (1966) and Thomas and Owen (1971).

Nitrite in neritic waters often shows marked differences with depth, and the concentration is usually somewhat less than that of ammonium (Vaccaro, 1965). Nitrite can be formed by bacteria through either the oxidation of ammonium or the reduction of nitrate. Phytoplankton can utilize nitrite as a source of nitrogen and have been shown to excrete extracellular nitrite when growing on high levels of nitrate (Vaccaro and Ryther, 1960; Carlucci, Hartwig, and Bowes, 1970).

In temperate coastal areas the distribution of nitrate in seawater usually shows a predictable seasonal pattern which is well documented (see Vaccaro, 1965). During the winter, vertical mixing and low rates of plant assimilation keep the nitrate concentration plentiful in near surface waters and rather uniform in vertical distribution. With the onset of spring, density stratification substantially reduces the vertical transfer of nitrate, and it is removed from the wind mixed surface waters via phytoplankton assimilation. Bacteria are probably responsible for regenerating nitrate through the oxidation of ammonium and nitrite (Harvey, 1966).

SAMPLE COLLECTION AND ANALYSIS

Samples were collected with PVC Van Dorn bottles off the coast of La Jolla, Calif., twice weekly from 7 February to 17 April 1970, at three stations in 50 m of water. Station II (Figure 1) was approximately 1 km directly seaward of Scripps Institution of Oceanography pier on the southern edge of Scripps Canyon, Station I was approximately 1.5 km SW of Station II on the southern edge of La Jolla Canyon, and Station III was approximately 1.5 km NW of Station II over the more gently sloping bottom north of both canyons. Water for the analysis of chemical and biological parameters was collected from the surface, 10, 20, 30, and 40 m depths at all three stations on each sampling day. Nutrient analyses were run on samples collected at Station II and alternately on those collected at Stations I and III (with a few exceptions). A Secchi disk reading and bathythermograph cast were always taken at Station II.

Immediately after sample collection, aliquots were drawn for oxygen determinations. They were "pickled" by the addition of the manganous sulphate and alkaline iodine solutions and were returned to the laboratory for the completion of the analysis. Within 2 hr after sample collection, aliquots were analyzed in duplicate for ammonium and urea while others were analyzed for chlorophyll *a* and phaeophytin *a*. Other aliquots were: 1) frozen and later analyzed (within 2 weeks) for nitrate, nitrite, silicate, and phosphate; 2) preserved for microscopic determination of phytoplankton species and numbers; and 3) stored (approximately 3 weeks) for salinity determinations.

The determinations of dissolved oxygen by a modified Winkler technique (Carritt and Carpenter, 1966), chlorophyll *a* and phaeophytin *a* by fluorometry (Holm-Hansen et al., 1965), nitrate by the cadmium-copper reduction and subsequent determination of nitrite (Wood, Armstrong, and Richards, 1967), nitrite by diazotization (Bendschneider and Robinson, 1952),

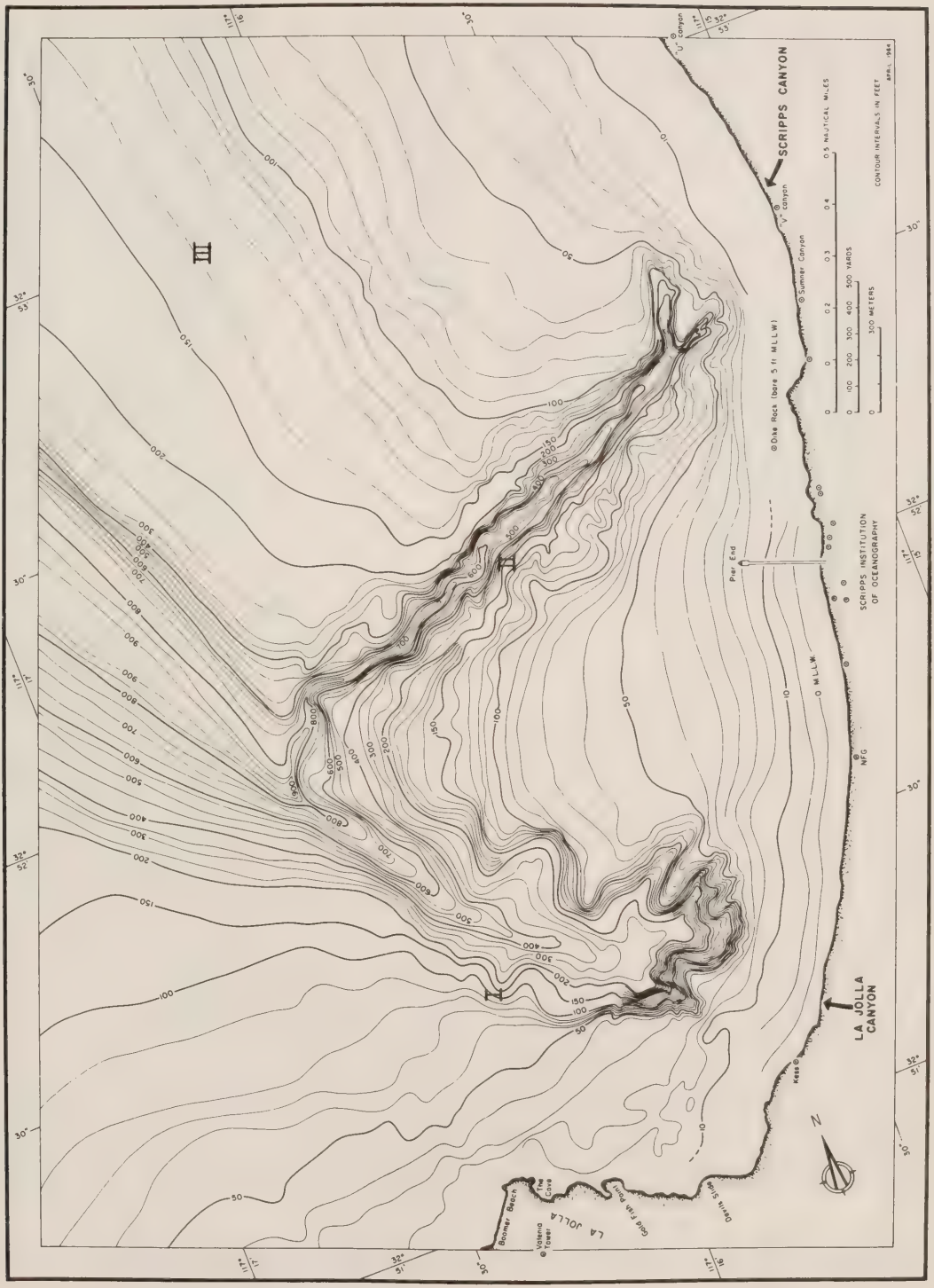

FIGURE 1.—The locations of Stations I, II, and III.

silicate by molybdate complexing (Mullin and Riley, 1955), and phosphate by molybdate complexing (Murphy and Riley, 1962) followed the procedures outlined by Strickland and Parsons (1968). Salinity was determined by conductivity measurements on an Autolab[R] salinometer.[3]

Ammonium was determined by the phenolhyochlorite method (Solórzano, 1969) and urea by the urease method (McCarthy, 1970), but both of these methods deserve additional comment. Solórzano states that for ammonium analyses the absorbance of samples is stable for at least 24 hr when a 0.5% sodium nitroprusside reagent is used, whereas, at higher concentrations a high and unstable blank which increases with time can result. Difficulties such as those expected at higher sodium nitroprusside concentrations were, however, occasionally experienced when using the recommended concentration. Efforts made to determine the source of this problem were complicated by its erratic occurrence, e.g., differences from day to day using the same reagents. No solution to the problem was found. It is, however, of little consequence when absorbances are read within a short interval of time, e.g., 15 min, since the optical density increased uniformly in blanks, samples, and standards. When analyzing as many as 50 samples at once, the reagent additions were staggered in time so that the absorbance of a sample was always read between 1.00 and 1.25 hr later.

A problem was encountered with the Worthington URC crude urease which was recommended for the urease method. Several batches of this product were purchased over a period of a year, and following the outlined purification procedure, the preparations were almost identical in activity and blank. Shortly after the urease-urea method was published (McCarthy, 1970), two batches of the same product were received which yielded both less activity and higher blanks than the preceding preparations. Owing to these difficulties, Sigma Type III urease was used subsequently. The resultant blank is higher (0.030-0.050 OD units/10-cm cell) than previously described and approximately 3 mg rather than 0.5 mg of the enzyme preparation must be added to each sample. A 0.1-0.2 ml Biopipette[R] was found to be accurate and rapid enough to permit direct addition of the concentrated enzyme preparation without dilution. In addition, it was found that by centrifuging the final urease preparation approximately 1,000 $\times$ g for 20 min and discarding the pellet, turbidity of the preparation could be reduced. For laboratory analyses of urea McCarthy (1970) recommended the use of aluminum foil coverings for the reaction vessels, but it should be noted that if the sample contacts the foil an erroneously high ammonium value will result. If foil coverings are used, care should be taken when moving the flasks, and they should be discarded after the addition of the oxidizing solution. After the addition of the last reagent, color will not result from ammonium added to the sample whereas contact with the aluminum foil will still interfere with the results.

The nutrient data were shown to depart from normality in distribution by plotting them on normal probability paper, so parametric statistics could not be applied. The Mann-Whitney U test (Tate and Clelland, 1957) was used for comparing medians from different stations or different periods. This test compares the central tendency of two distributions and does not assume similarity in variance. The Tukey-Siegel modification of the Mann-Whitney U test was used to compare variability between sets of data, the median regression procedure (Tate and Clelland, 1957) was used to calculate the regression lines, and the *tau* coefficient test (Kendall, 1955) was used to determine correlations. The α for significant differences was taken at the 0.05 level except when there was multiple testing, in which cases $0.05/n$ was used where n = the number of times a test was run with interrelated data.

The data for dissolved oxygen, chlorophyll *a*, phaeophytin *a*, silicate, phosphate, phytoplankton species and numbers, temperature, and salinity will be reported elsewhere (Kamykowski).[4]

[3] Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

[4] Kamykowski, D. Some physical and chemical aspects of the phytoplankton ecology off La Jolla, California. Manuscript in preparation.

RESULTS

Representative plots of the nutrient data are shown in Figures 2 and 3. The nitrate concentrations consistently increased with depth. When a thermocline was present, the median nitrate concentration above was 0.49 μg at. N/liter while that below was 12.81 μ at. N/liter. The median nitrite concentration above the thermocline was 0.04 μg at. N/liter while that below was 0.36 μg at. N/liter. The median ammonium concentration above the thermocline was 0.09 μg at. N/liter while that below was 0.34 μg at. N/liter. Both the medians and the variabilities for nitrate, nitrite, and ammonium concentrations above the thermocline were significantly different from those below. The median urea concentration above the thermocline was 0.16 μg at. N/liter while that below was 0.12 μg at. N/liter, and neither the medians nor the variabilities were significantly different.

Urea data for stations made on the same day are plotted in Figure 4. We first noticed that the urea values appeared to vary markedly from one month to another, and since elasmobranches excrete nitrogen primarily as urea (Baldwin, 1964), this pattern suggested that the quantity of urea in the water may have been affected by a heavy infestation of 1-2 m long blue sharks (*Prionace glauca*). The infestation was first noted on 28 February, and initially one could see a few tens of dorsal fins extending above the surface at any time in the vicinity of any of the stations. After a few days the sharks became much more wary of the skiff and although they remained in great numbers, they were usually deeper. Shark sightings continued to be numerous until 21 March and thereafter they were rare. The periods before (7-24 February), during (28 February-21 March), and after (24 March-17 April) the infestation, hereafter referred to as Periods A, B, and C, are indicated in Figure 4. These periods define an initial stage of low urea values, a secondary stage of higher and more variable urea values, and a final stage which appears similar to the first. Medians and ranges for nitrate, nitrite, ammonium, and urea for the three periods are given in Table 1 and were used for the statistical analyses reported in Tables 2, 3, and 4. The highest concentration of urea detected at any time during the sampling program, 1.28 μg at. N/liter, was in a surface sample collected approximately 1 m from a 2½-m blue shark which was near Station I.

Comparisons between Periods A, B, and C Table 4) show that the periods differed with respect to nitrate, nitrite, and ammonium as well as urea. The median nitrate concentration in Period B was significantly lower than those in either Period A or Period C. The median nitrite concentrations were similar for all three periods. The median ammonium concentration for Period C was significantly lower than that for Period A. The median urea concentration for Period B was significantly higher than those for either Period A or Period C. Both the variability and the range of urea concentrations were considerably higher in Period B than in either Period A or Period C.

TABLE 1.—Medians, ranges, and number of samples for nitrate, nitrite, ammonium, and urea within each period. The medians and ranges for each form of nitrogen are in units of μg at. N/liter.

	Nitrate			Nitrite			Ammonium			Urea		
	Median	Range	Number	Median	Range	Number	Median	Range	Number	Median	Range	Number
Period A												
Stations I and III	6.91	0.50-19.07	20	0.25	0.04-0.36	20	0.29	0.00-0.71	20	0.09	0.00-0.18	20
Station II	6.87	0.53-19.00	20	0.21	0.05-0.44	20	0.27	0.00-0.73	20	0.03	0.00-0.25	20
All values	6.58	0.50-19.07	40	0.24	0.04-0.44	40	0.28	0.00-0.73	40	0.07	0.00-0.25	40
Period B												
Stations I and III	0.88	0.00-15.11	30	0.12	0.00-0.61	30	0.21	0.00-1.96	30	0.22	0.00-0.67	30
Station II	1.81	0.00-15.00	30	0.14	0.00-0.58	30	0.25	0.00-1.66	30	0.28	0.00-0.90	30
All values	0.88	0.00-15.11	60	0.13	0.00-0.61	60	0.23	0.00-1.96	60	0.27	0.00-0.90	60
Period C												
Stations I and III	9.43	0.09-23.16	35	0.20	0.00-0.88	35	0.06	0.00-0.59	35	0.09	0.00-0.24	35
Station II	10.09	0.00-20.87	35	0.25	0.00-0.73	35	0.09	0.00-2.38	35	0.12	0.00-0.56	35
All values	9.64	0.00-23.16	70	0.22	0.00-0.88	70	0.08	0.00-2.38	70	0.12	0.00-0.56	70

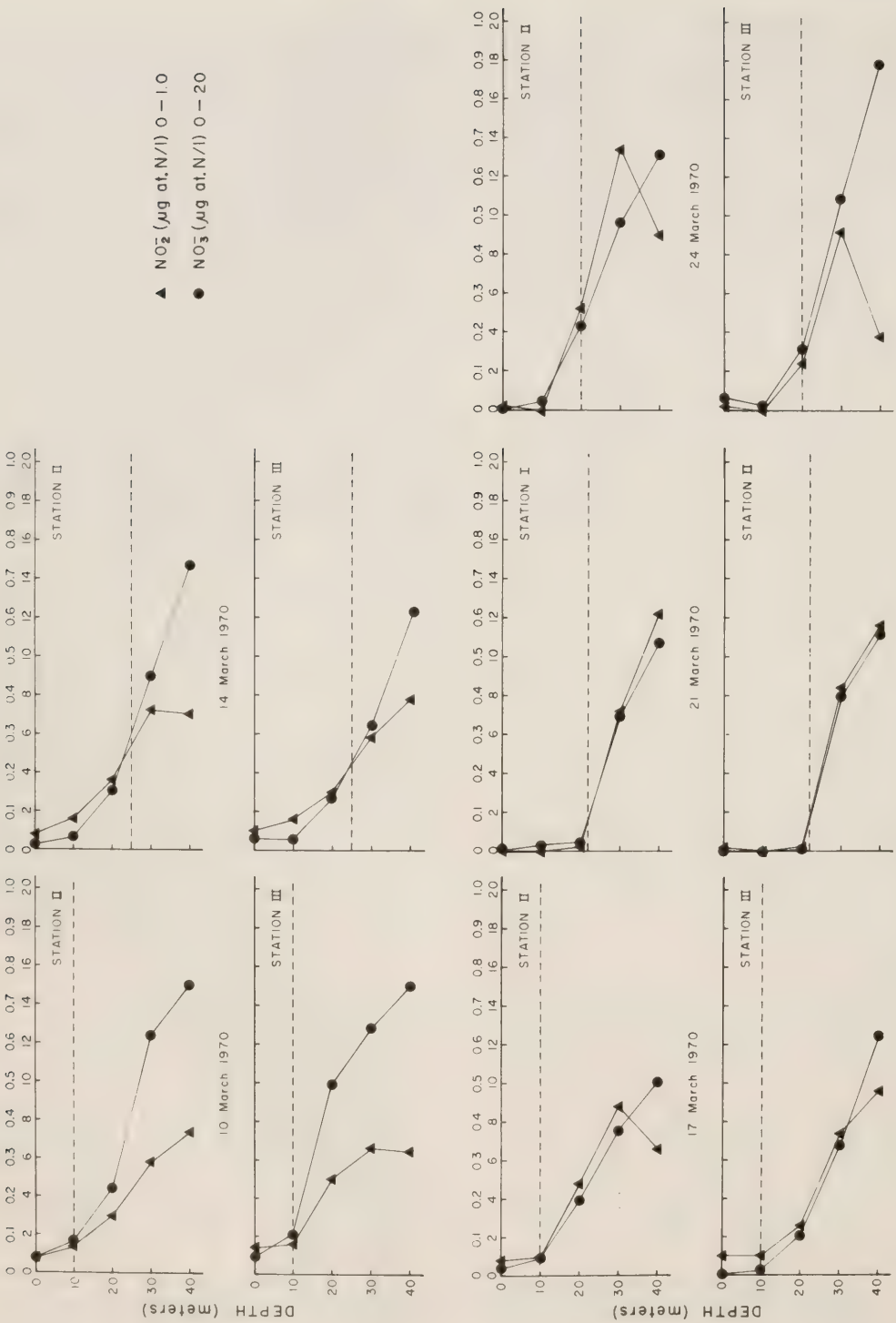

FIGURE 2.—Nitrate and nitrite concentrations for paired stations on five successive sampling days. The depth of the thermocline is indicated by the dashed line.

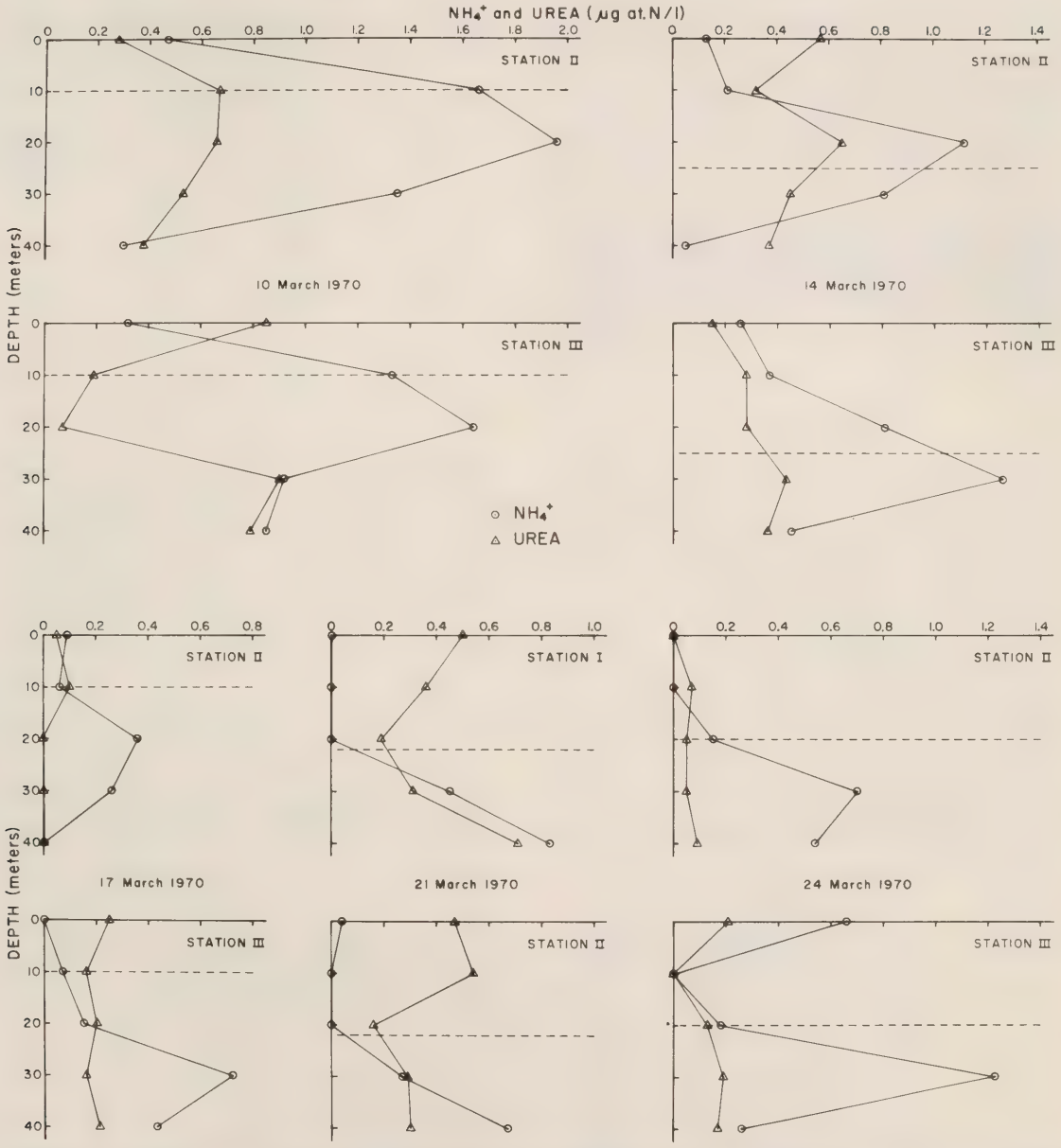

FIGURE 3.—Ammonium and urea concentrations for paired stations on five successive sampling days. The depth of the thermocline is indicated by the dashed line.

The *tau* coefficient was used to examine ammonium and urea concentrations for correlation in each of the three periods. From the z approximation the following pattern emerged: for Period A there was no correlation ($P = 0.030$), for Period B the correlation was positive ($P = 0.009$), and for Period C there was no correlation ($P = 0.124$). Values for the probabilities

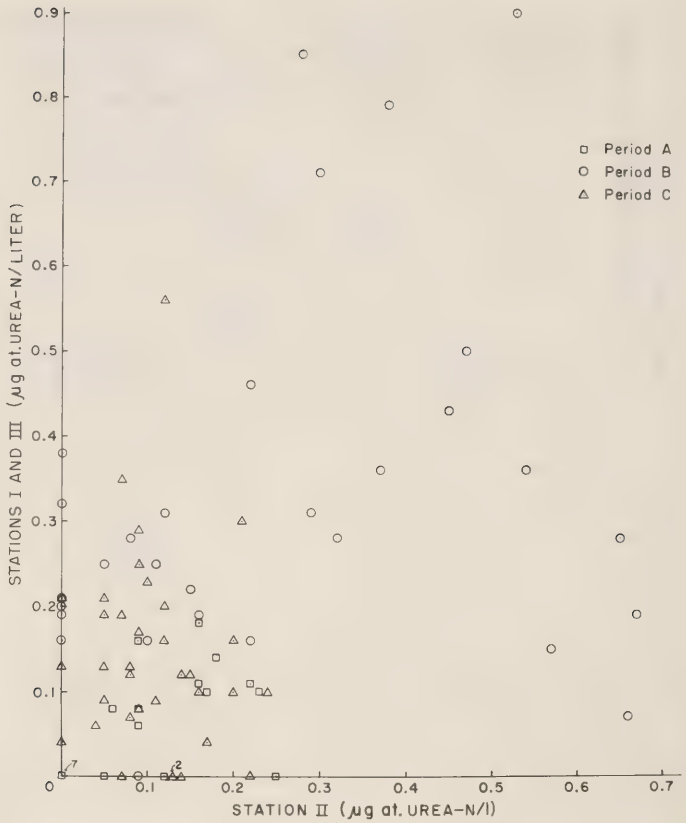

FIGURE 4.—Urea concentrations at the same depth for paired stations sampled on the same day during Period A, Period B, and Period C.

TABLE 2.—Linear regressions of Station I or III vs. Station II for nitrate, nitrite, ammonium, and urea within each period.

Nutrient	Period	Station I or III vs. Station II	P[1]
Nitrate	A	$Y = 1.00X + 0.50$	<0.05
	B	$Y = 0.99X - 0.05$	<0.05
	C	$Y = 0.97X + 1.00$	<0.05
Nitrite	A	$Y = 0.98X + 0.02$	<0.05
	B	$Y = 0.92X + 0.00$	<0.05
	C	$Y = 0.90X + 0.03$	<0.05
Ammonium	A	$Y = 1.10X - 0.02$	<0.05
	B	$Y = 1.76X + 0.17$	<0.05
	C	$Y = 1.42X + 0.02$	<0.05
Urea	A	$Y = 0.65X - 0.02$	<0.05
	B	$Y = 0.52X + 0.16$	>0.05
	C	$Y = 2.00X - 0.06$	>0.20

[1] Probability that the regression slope is not different from zero.

are for the two-sided test and since these same data will be used for another analysis the level of significance (α) is taken as 0.05/2.

Vaccaro and Ryther (1960) observed maximum concentrations of nitrite when both phytoplankton and nitrate were abundant at light limiting depths. *Tau* coefficients indicated that in the present study there were no significant correlations between either 1) the median chlorophyll *a* and the median nitrite concentrations below the thermocline ($P = 0.288$) or 2) the chlorophyll *a* and the nitrite concentrations at or within 5 m of the thermocline ($P = 0.490$).

Lorenzen (1967) suggested that a phaeo-pigment/chlorophyll ratio is indicative of herbivore grazing pressure, and since ammonium is the major nitrogenous excretion product of most marine crustaceans (Parry, 1960), we used the *tau* coefficient to examine the phaeo-pigment/chlorophyll ratios and ammonium and urea data from this study for positive correlation. If one assumes that the single pigment profile taken each sampling day is representative of the whole area

TABLE 3.—Comparisons of medians and variability of the nitrate, nitrite, ammonium, and urea results from stations sampled on the same day.

Nutrient	Period	Medians P	Variability P
Nitrate	A	>0.70	>0.40
	B	>0.70	<0.05
	C	>0.40	>0.20
Nitrite	A	>0.40	>0.70
	B	>0.70	>0.40
	C	>0.90	<0.05
Ammonium	A	>0.90	>0.90
	B	>0.40	>0.60
	C	>0.60	>0.10
Urea	A	>0.20	>0.90
	B	>0.10	<0.05
	C	>0.20	>0.60

for that day, it is reasonable to compare the phaeo-pigment/chlorophyll ratios with the best estimate of average ammonium and urea values for the same area. This is supported by the findings that the phytoplankton species composition was similar at all three stations and that the surface chlorophyll concentrations at Stations I and III were significantly correlated with the surface cell counts at Station II. Thus we paired the phaeo-pigment/chlorophyll ratios with the median ammonium and urea values at each depth for the same day in the following analysis. The phaeo-pigment/chlorophyll ratios were not correlated with the median ammonium concentrations in either Period A ($P = 0.189$) or Period C ($P = 0.171$) but were positively correlated in Period B ($P < 0.001$). The phaeo-pigment/chlorophyll ratios were not correlated with the median urea concentrations in Period A ($P = 0.382$), Period B ($P = 0.397$), or Period C ($P = 0.166$). Since each set of pigment and nutrient data have been used in two correlations, an appropriate α for significance is 0.05/2. Scatter diagrams for phaeo-pigment/chlorophyll ratios and the median ammonium and urea concentrations are presented in Figures 5 and 6 respectively.

DISCUSSION

Earlier studies in the Peru Current (McCarthy, 1970), in the central Pacific (McCarthy, 1971), and the present study have shown that great differences in both ammonium and urea occur on a vertical scale of a few meters. If during this study a small-scale inhomogeniety had been prevalent in the horizontal as well as vertical dimensions, it should have been evident both within and between stations made on the same day. If, on the other hand, there had been horizontal patches large with respect to a 1.5 km distance, the concentration at a particular depth should have been similar at both stations; this was apparently the case for nitrate, nitrite, and

TABLE 4.—Normal deviates (z) and corresponding probabilities (P) for comparisons between medians and variabilities of nitrate, nitrite, ammonium, and urea for all three periods.

Nutrient	Periods	Medians		Variabilities	
		z	P[1]	z	P[1]
Nitrate	A vs. B	3.80	**<0.005**	3.12	**<0.005**
	A vs. C	0.37	0.712	3.17	**<0.005**
	B vs. C	3.82	**<0.005**	2.72	**<0.005**
Nitrite	A vs. B	1.68	0.083	0.60	0.549
	A vs. C	0.48	0.631	4.89	**<0.005**
	B vs. C	1.83	0.067	2.31	**0.021**
Ammonium	A vs. B	0.57	0.569	2.36	**0.018**
	A vs. C	3.19	**<0.005**	1.40	0.162
	B vs. C	2.14	0.032	3.98	**<0.005**
Urea	A vs. B	5.58	**<0.005**	4.90	**<0.005**
	A vs. C	2.74	**<0.005**	1.02	0.308
	B vs. C	5.02	**<0.005**	4.97	**<0.005**

[1] P values are given for the two-sided test. To correct for multiple testing an α of 0.05/2 should be used. Significant differences are in bold type.

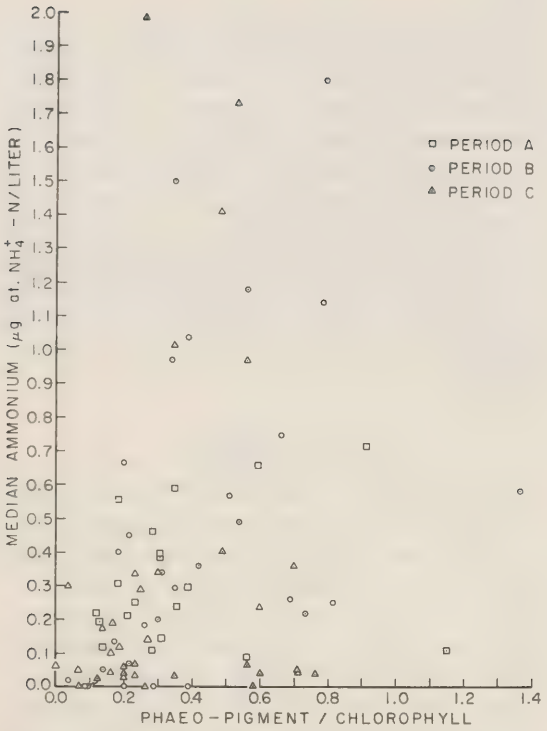

FIGURE 5.—Median ammonium concentrations and phaeopigment/chlorophyll ratios for Period A, Period B, and Period C.

to a lesser degree for ammonium but was not the case for urea.

Table 2 shows that the slopes for nitrate, nitrite, and ammonium regression equations contrasting the two stations sampled on any one day are positive and are significantly different from zero for each period. This implies that the values observed at each depth at one station on a particular day are positively correlated with those at corresponding depths at the other station. This resulted because the nitrate and nitrite profiles were nearly identical for the two stations on a single day and the ammonium profiles generally resembled each other. The regression slopes for the nitrate and nitrite data were all similar to 1.0, but the ammonium and urea slopes were occasionally far from unity. The regression slopes for the urea data were not significantly different from zero for either Period B or Period C. This analysis indicates that the patch structure of urea distribution is probably of a smaller horizontal scale than that of nitrate, nitrite, or ammonium. In comparing a particular depth at one station with the corresponding depth at another station, the two urea values are less likely to be similar than the ammonium values and considerably less than the nitrate or nitrite values.

The similarity of median values for the station pairs sampled on the same day (Table 3) suggests, on the other hand, a homogenous distribution for each nutrient over the sampling area; however, the stations showed markedly more resemblance in nitrate, nitrite, and ammonium than in urea. Comparisons also showed that within each period the median at Stations I and III were not different. This further supports the hypothesis of a smaller patch structure for urea since there was no persistent difference between stations with respect to urea, even though on any one day the stations may have differed significantly.

The three periods were based on the timing

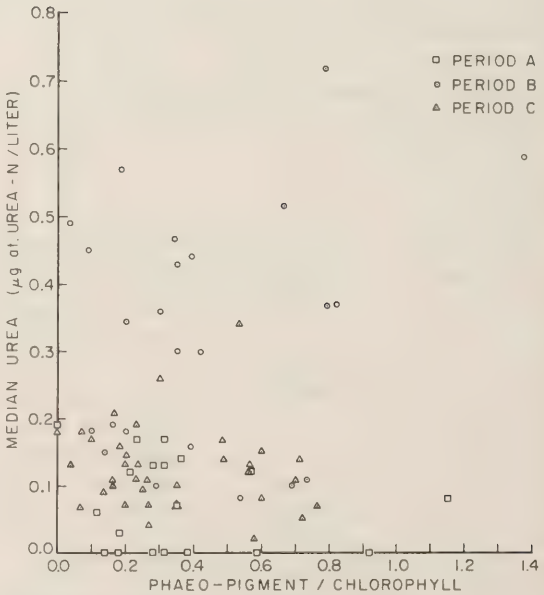

FIGURE 6.—Median urea concentrations and phaeo-pigment/chlorophyll ratios for Period A, Period B, and Period C.

of the shark infestation, and it is evident that the urea values were elevated significantly during Period B. It is unlikely that the significant differences in the medians and variabilities of the nitrate, nitrite, and ammonium values between periods were related to the presence of the sharks per se. The trends for each nutrient were markedly different: For nitrate the Period B median concentration was less than that in either Period A or Period C, for nitrite the median was unchanged, and for ammonium the median in Period B was greater than that in Period C but not different from that in Period A. Kamykowski (see footnote 4) presents data which suggests that a mechanism involving internal waves acting together with intermittent wind-related events (e.g., upwelling) can explain the pattern of increases in surface nitrate and corresponding decreases in surface temperature found in the study. Strasburg (1958) has shown that blue sharks in the central Pacific Ocean were found most frequently where the temperature was between 7° and 15°C; however, the temperature differences with respect to either time or depth which were encountered during the present study were not sufficient to provide an explanation for the shark infestation.

The nitrite regression equations contrasting the two stations sampled on the same day reveal that the dynamics of the nitrite production and utilization is uniform over the scale of a few kilometers. If the greater nitrite concentration below the thermocline represents a greater rate of production, our finding is consistent with the ideas put forth by Vaccaro and Ryther (1960) which suggest that nitrite liberation by phytoplankton in the presence of excess nitrate will be intensified at reduced light levels. The lack of correlation between the chlorophyll *a* and nitrite concentrations, however, implicates a complex interaction between components of the nitrite system.

The lack of correlation between ammonium and urea concentrations for Period A and Period C follows the pattern seen earlier in data from the English Channel (Newell, 1967), the Peru Current (McCarthy, 1970), and the central Pacific (McCarthy, 1971), but the strong positive correlation in Period B deserves further consideration. The median ammonium values for Periods A and B were not different, and although the rates must have been similarly balanced, the sources as well as rates of both supply and utilization could have been considerably different for the two periods. If the shark infestation was responsible for the elevated urea concentrations during this period, was it perhaps not also responsible for enough of the ammonium present to have produced the observed relationship? It would seem unlikely that the sharks were directly responsible since the selachii (modern sharks) are reported to excrete 80-90% of their nitrogenous end products as urea, 2-10% as ammonium, and the balance as amino acids and an unidentified fraction (Scheer, 1963). During Period B a squid (*Loligo opalescens*) spawn was noted off the coast of La Jolla. These usually last approximately 1 week, and during this time the adult squid reportedly do not feed (A. O. Flechsig, personal communication). Sharks collected during this period were found to have been feeding on squid (N. Marshall and G. Sullivan, personal communications), but it seems unlikely that the sharks were attracted to this area by the squid since such spawns are frequently noted without the presence of sharks. The squid spawns do, however, regularly attract birds (*Larus* spp.), and we also noted greater abundances of birds during this time. Nitrogen is excreted principally as ammonium by cephalopods (Barnes, 1963) and as uric acid by birds (Needham, 1931). It has been reported that uric acid is unstable in seawater and rapidly degrades to urea (Williams, 1970)[5] so the birds might have been an additional source of urea.

It is therefore possible that Period B was also unique with respect to the presence of ammoniotelic organisms which were either directly or indirectly supporting or supported by the shark population and which were in sufficient abundances to have resulted in the positive correlation between ammonium and urea concentrations.

[5] Williams, P. M. 1970. The stability of organic nitrogen compounds in seawater. University of California, Institute of Marine Resources. Research on the marine food chain progress report for U.S. Atomic Energy Commission Contract At(11-1)GEN 10, P.A. 20. Part 1, p. 8b. [Unpubl. manuscr.]

The strong positive correlation between phaeo-pigment/chlorophyll ratios and ammonium concentrations in Period B suggests that ammoniotelic herbivores were important, and perhaps the presence or abundances of these organisms were also related to the shark presence.

Another possible explanation for the positive correlation between ammonium and urea concentrations is that bacterial hydrolysis of urea during Period B was responsible for increased ammonium production. ZoBell and Feltham (1935) isolated marine bacteria capable of hydrolyzing urea from the same area used for the present study, but indirect evidence (McCarthy, in press) indicates that bacterial hydrolysis is probably of much less importance than phytoplankton uptake in the fate of urea in near surface waters off the coast of Southern California.

Fish, zooplankton, and phytoplankton have long been known to occur in schools, patches, and layers in near surface waters, and their spatial array probably contributed to the irregular distributions of both ammonium and urea seen in this study. On a scale of a few meters the input due to zooplankton and the utilization due to phytoplankton may approach an equilibrium, but the immediate effect of a large fish or fish school passing through a particular volume would be elevated ammonium and urea concentrations which would decrease with time at rates dependent on both diffusion and biological utilization. Since the blue shark has no urinary sinus (Dr. T. Enns, personal communication), both the branchial and the renal systems would be expected to release urea continuously. One can calculate both branchial (Boylan, 1967) and renal (Forster, 1967) excretion rates for *Squalus*, but it is questionable whether these rates would be representative of *Prionace glauca*. The major problem in attempting to estimate the shark urea production during the present study is, however, that of reliably estimating the shark biomass.

An increased rate of ammonium or urea production in a parcel of water will not necessarily be reflected in an increased seawater concentration of the metabolite. To the extent that rates of utilization are dependent on substrate concentrations, e.g., nitrogen uptake by phytoplankton, then an immediate increase in the rate of utilization might be expected in response to an increased rate of production. There are no sewage outfalls in the vicinity of La Jolla Bay, but the supply of ammonium and/or urea to waters proximate to such discharges may result in significant enrichment with these nutrients (Eppley et al., in press).

Because of the spatial variability in both supply and utilization and the low concentrations usually encountered, it is difficult to interpret, or even detect, short-term changes in ammonium and urea concentrations in near-surface seawater. Surface waters into which fish and crustaceans migrate daily in some degree of synchrony to feed is one setting in which such changes might be expected, and have been observed. Beers and Kelly (1965) presented data which suggested a correlation between variations in ammonium concentrations in the upper 500 m of the Sargasso Sea and the diurnal migration of zooplankton, and Emmet (1969) referred to unpublished work which showed that a diurnal maximum in urea concentration occurs in open ocean surface waters early in the morning.

If, as Lorenzen (1967) has suggested, a phaeo-pigment/chlorophyll ratio is indicative of herbivore grazing pressure, the significant correlation between this ratio and ammonium concentrations reported in Period B of this study might imply that (1) both fecal material and ammonium excreted by herbiverous zooplankton have residence times which are similar, or (2) ammonium is released with the degradation of herbivore fecal pellets. The lack of correlation in Periods A and C might imply that herbivores were not significant sources of ammonium during these periods. The lack of correlation between phaeo-pigment/chlorophyll ratios and urea concentrations might imply that (1) herbivore excretion is not an important source of urea, (2) the residence times of phaeo-pigments and urea are sufficiently different to mask any association, (3) urea excreted by nonherbivores obscured a relationship between phaeo-pigment/chlorophyll ratios and urea concentrations, or (4) urea is not released with the degradation of herbivore fecal pellets. Herbivores zooplankton have been shown to release substantial quantities

of urea (Corner and Newell, 1967; McCarthy, 1971) so the lack of correlation with phaeo-pigments might further implicate the blue sharks as the major source of urea during Period B. The residence times of ammonium and urea may well differ since ammonium is utilized readily by all marine phytoplankters whereas urea is utilized by only some species and even then uptake may be partially suppressed by certain concentrations of nitrate or ammonium (McCarthy and Eppley, in press). It is not known whether urea is released in fecal pellet degradation.

The data from the present study do not show whether the relationship between the presence of the blue sharks and the elevated urea values in Period B is one of cause and effect. If the sharks were a significant source of urea, this may provide an explanation for the similarity in urea concentrations above and below the thermocline, the more irregular distribution of urea, and perhaps the lack of correlation between phaeo-pigment/chlorophyll ratios and urea concentrations. Without estimates of urea input due to excretion by sharks, other fish, zooplankton, and possibly birds, and rates of urea utilization for phytoplankton, the net effect of the shark population's contribution to urea production cannot be rigorously evaluated.

While this manuscript was in review, Remsen (1971) published the results of urea analyses for samples collected from both the eastern tropical Pacific Ocean and coastal waters off northeastern United States. The concentrations he detected were generally higher than those reported either previously or in this communication but his conclusions as to the biological significance of urea in the marine environment are not at variance with those presented here

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FISH SOLUBLES AS A PARTIAL SUBSTITUTE FOR MILK AND MILK BY-PRODUCTS IN LIQUID RATIONS FOR NEONATAL ANIMALS

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ABSTRACT

This paper presents (1) a literature review of the use of fish protein in milk replacers for neonatal animals, (2) a list of criteria for proteins used in milk replacers, and (3) reports on three experiments in which menhaden fish solubles were partially substituted for milk protein in milk replacer rations.

Initial experiments reported here indicated that low levels (5%) of fish solubles produced equal calf growth when they replaced a similar amount of milk products in veal calf rations. However, the addition of 15% freeze-dried solubles at the expense of dried skim milk (DSM) did not produce satisfactory growth in young lambs. This was true even when lecithinated soy flour or delactosed whey powder supplemented part of the protein in the ration. Therefore, it is concluded that if significant quantities of fish protein are to be incorporated into milk replacer rations, protein of higher quality than that present in fish solubles must be used.

Attempts to develop a product suitable for replacing fresh whole milk for feeding calves occurred in the early 1900's. However, due to the lack of knowledge regarding calf nutrition, these products were not very satisfactory. By the end of the 1940's knowledge of the nutritional needs of calves had developed to a point that made it possible for satisfactory substitutes for whole milk to be marketed. Today, milk replacers have been refined to such an extent that many dairymen are reporting faster weight gains by feeding milk replacers instead of fresh whole milk. Several important developments contributed to this improved performance. They include: (1) the use of antibiotics, (2) the use of stabilized vitamins, and (3) the increased use of dried milk proteins. Recently the use of milk replacers has increased because of automation of feeding techniques, their ease of handling and storing, improved formulations, and the increased emphasis on salvaging orphan and runt animals which would have previously have been lost by the producer.

Manufacturers of milk replacers depend largely upon dried skim milk (DSM) and dried whey as the major ingredients. Because of the continued high market price of DSM throughout the world, feed manufacturers are looking for lower priced substitutes to be used in their milk replacer formulations. The superior value of feeding milk solids as compared to vegetable feedstuffs in milk replacers has been well demonstrated (Huber, 1965). Therefore, it is the purpose of this paper (1) to briefly review work reported in the literature, (2) to list the criteria necessary for proteins used in milk replacers, and (3) to report the results of our work to determine if fish solubles can be partially substituted for milk and milk products in liquid rations for neonatal animals.

REVIEW OF RECENT LITERATURE

Harshbarger and Gelwicks (1965) reported that calves fed a milk replacer containing 20% low-fat fish meal performed as well as calves that were receiving a 50% DSM replacer. Average daily gains and feed intakes at 12 weeks of age were similar for all calves studied that received either DSM or fish meal.

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Huber and Slade (1967) substituted varying levels of fish protein (defatted fish meal) for skim milk protein in calf milk replacers in growth and balance studies. They also investigated the effect of varying levels of dietary fat in combination with fish protein on growth response. Their data showed that average daily gains and feed efficiencies were not significantly different when fish protein replaced up to 40% of the dietary protein. However, when fish protein replaced from 60 to 67% of the dietary protein, significant decreases ($P<0.01$) occurred. Increasing fat in the rations from a 10 to 20% level caused a linear increase ($P<0.05$) in gains. However, no interaction between protein source and fat level was detected. Furthermore, as the amount of fish protein in the milk replacer increased, digestibilities of dry matter, crude protein, fat, and ash decreased. Only when fish protein furnished 100% of the dietary protein was there a significant depression ($P<0.05$) in the percent of digested nitrogen retained. Crude protein in the fish concentrate was reported to be 80% digestible compared to 90% for skim milk protein.

Williams and Rust (1968) reported a study with four different formulations of experimental milk replacers, and their results supported the findings of Huber and Slade (1967). Defatted fish flour provided from 14 to 42% of the total protein in these experimental rations. Total protein, fat, and digestible nutrients were equal in all experimental rations and were similar to those of the standard milk replacer ration. At the termination of the 42-day experiment, they reported that calves fed the various experimental milk replacers gained similar amounts of weight and they were comparable to calves on the conventional milk replacer. These results indicated that fish protein could be effectively utilized and provide up to 42% of the protein in the ration.

Gorrill (1970) conducted similar studies on the use of fish protein in milk replacers. Fish protein concentrate (FPC), which was in this case isopropanol extracted fresh whole herring, accounted for 50% of the protein in the fish containing milk replacer. He also fed a dry starter on a restricted basis and hay ad lib. with the liquid diet and found that at least 50% of the milk replacer protein could be supplied by FPC with no significant difference in weight gains from those of whole milk or an all-milk product replacer ration.

In European countries there has been increasing interest in developing fish products which could be utilized in milk replacer rations. France is currently producing 550,000 to 600,000 tons of milk replacer per year which includes the use of fish protein in veal diets. In particular, two French feed manufacturers began marketing milk replacers containing fish protein in the form of FPC or autolyzed fish concentrate in an effort to use a lower priced animal protein.

CRITERIA FOR PROTEINS IN MILK REPLACERS

Generally, there are eight criteria that will have to be met by the producers of fish protein before feed manufacturers will consider using such protein in milk replacer formulas.

First, the fish protein must be highly available to the animal. At present, a wide range of values has been reported on fish protein in milk replacer rations. Reports of from 50 to 80% digestible protein can be found in the literature. Since skim milk has a digestible protein value of about 90%, it is imperative that fish products have a protein digestibility as close to this as possible.

Second, the product must be of uniform quality and be available throughout the year in quantities large enough to meet demands.

Third, fish protein must be lower in cost than milk protein or equal if DSM is scarce. Manufacturers will be willing to use fish protein only if its substitution for milk products gives a reduction in price of the milk replacer. There is always risk involved when changing formulas, and the manufacturers must be shown an economic advantage before they will take that risk.

Fourth, the fish protein must be suspendable in water when used in the formulation. With the increased application of automatic feeding devices in the rearing of neonatal animals, a completely suspendable milk replacer is important. The functional properties of current FPC and

fish meals must be improved to develop a product that will remain in suspension.

Fifth, fish proteins must be odorless, relatively free from a fishy taste, have a light color, and be stable. Many manufacturers of milk replacers feel that the fat content of the fish product must be kept as low as possible (less than 1%) to maintain the stability of fish protein. Some manufacturers suggest additions of antioxidant since they have experienced a deterioration of autolysates after storage. However, it has been reported by Ronning (1970) that hydrogenated fish oils with an iodine number of 80 are of value in high-energy milk replacers. Through the addition of higher levels of α-tocopherol (Vitamin E) and by reducing the levels of unsaturated fatty acids by hydrogenation, he was able to feed calves up to 26.2% fish oil with no detrimental effects.

Sixth, the bone content of the fish protein product must be relatively low. Producers of milk replacers indicate they want a final product with less than a 10% mineral content. More importantly, they want this concentration of minerals to remain constant from one batch of milk replacers to another. Therefore, the major individual ingredients in the milk replacer must have a constant mineral composition. In addition, if a milk replacer containing fish protein is to be fed for the production of veal calves, it must be low in iron (less than 50 ppm). The preferred paleness of veal muscle tissue results from a state of anemia due to the low iron content of the rations fed to veal calves. At present, the iron content of FPC made by isopropyl alcohol extraction may vary between 147 and 770 ppm (Finch, 1970). However, a large part of this iron comes from mechanical contamination (i.e., grinding) and may be of a type that is poorly available to animals. If the iron content can be made unavailable by adding an iron-chelating agent, as suggested by Saheb and Charpentier (1970), a high-quality veal meat may be produced. Inasmuch as the major market in the United States is for replacement animals, iron should not be a problem.

Seventh, the moisture content of the fish protein must be kept low to prevent lumping of the milk replacer and other texture changes during storage. Most milk replacers contain 5% moisture or less.

Eighth, fish protein to be used in milk replacers would have to have a reasonably low bacterial plate count because neonatal animals are quite susceptible to digestive upsets. A low moisture content would help to keep bacterial growth to a minimum.

EXPERIMENTAL RESULTS

Our research at the National Marine Fisheries Service, College Park Laboratory was conducted to determine the feasibility of using fish solubles in milk replacer rations.

EXPERIMENT I

The objective of the first study was to determine the effect of partially substituting condensed menhaden fish solubles in a commercial ration for veal calves. Four Holstein bull calves were placed individually in stalls at 3 days of age. Two of the calves were fed a commercial veal ration, containing 24% protein and 20% fat. The remaining two calves received the same commercial ration with low-fat (3%) menhaden fish solubles replacing 5% of the ration on an equal weight basis. The calves were full-fed twice daily. Table 1 shows the results of this experiment. At 75 days of age, the milk replacer plus fish solubles group had average daily weight gains (0.93 kg) and feed conversions (1.41) comparable to those of the all-milk products replacer. However, due to the small number of

TABLE 1.—Experiment I. Weight gains and feed consumptions of calves fed either control milk replacers or milk replacers containing 5% fish solubles.

	Control	Fish solubles
Average body weight, kg		
Initial	39.09	36.82
75 days	105.00	106.36
Average daily weight gain, kg		
36 days	0.82	0.72
75 days	0.88	0.93
Average feed (dry)/gain		
36 days	1.09	1.20
75 days	1.53	1.41

animals used in this study it cannot be interpreted clearly that supplementation with fish solubles produced a superior product, but it is apparent that when fish solubles replaced 5% of an all-milk replacer commercial ration, growth rates and feed conversions were at least equal to the control that contained all-milk protein.

A triangular organoleptic test for flavor with 12 panelists was performed on 1.91-cm slices from the liver, loin ends (chops), and rounds (cutlets) of all test animals. Table 2 shows the results of the organoleptic evaluations. When the data from this test were statistically analyzed by the Student's t-test, a significant flavor difference ($P<0.05$) was found between the two groups. Meat from the experimental animals appeared to have more beef flavor rather than the desirable bland flavor associated with veal. Likewise, the meat from the experimental animals had a noticeably darker color than that of the control animals. This difference was probably due to the high level of minerals present in the fish solubles, especially iron.

TABLE 2.—Experiment I. Flavor test of meat from veal calves fed either control milk replacers or milk replacers containing 5% fish solubles.

	Control	Fish solubles
Cutlet		
Replication I	[1]7.67 ± 1.07	6.00 ± 1.71
Replication II	6.50 ± 1.88	6.00 ± 1.41
Average	[2]7.08 ± 1.61	6.00 ± 1.53
Chops		
Replication I	7.92 ± 1.00	6.50 ± 2.20
Replication II	7.42 ± 1.56	6.25 ± 1.86
Average	[2]7.67 ± 1.31	6.38 ± 2.00
Liver		
Replication I	6.25 ± 1.91	6.67 ± 1.83
Replication II	5.92 ± 2.19	6.33 ± 1.83
Average	6.08 ± 2.02	6.50 ± 1.79

[1] All values represent a scale of from one (unacceptable flavor) to eight (highly acceptable flavor).
[2] Significant at $P<0.05$.

EXPERIMENT II

The objective of this experiment was to study the feasibility of supplementing dried whey product, DSM, and/or soy flour with dry, low-fat menhaden solubles in lamb rations. Fifteen crossbred lambs, 2 to 7 days old, were placed on a commercial liquid, all-milk replacer ration for a preliminary period of 1 week. At the end of this period, lambs were allotted by weight, sex, and age to one of three experimental rations. The composition of the rations is shown in Table 3. All rations contained 24% protein, 20% fat, vitamins, minerals, antibiotic, and antioxidant. All lambs were given as much liquid feed as they could consume twice daily. Every 7 days body weights were measured, and feed consumption data were recorded daily. The experiment was terminated after 28 days. The average weight gains are shown in Table 4. Ration II (soy, whey product, and fish solubles) produced a growth response equal to 28.6% of that of Ration I (DSM and whey product), and Ration III produced an 82.9% response compared with Ration I.

TABLE 3.—Lamb ration formulations used in Experiments II and III.

Ingredients	Ration I	Ration II	Ration III
	%	%	%
Dried skim milk	65.00	--	30.00
Whey product	3.80	29.74	19.90
Menhaden fish solubles (freeze-dried)	--	15.00	15.00
Lecithinated soy flour	--	20.00	--
Glucose[1]	8.32	16.47	13.02
Emulsified lard	19.63	15.54	18.83
Vitamin premix[2]	1.00	1.00	1.00
Mineral premix[3]	1.00	1.00	1.00
Antibiotic premix[4]	1.00	1.00	1.00
Antioxidant premix[5]	0.25	0.25	0.25
	100.00	100.00	100.00

[1] Cerelose, Corn Products Co., New York. (Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.)
[2] Vitamin premix provides per kilogram ration: A, 3,300 IU; E, 22 IU; D_3, 66 IU; B_{12}, 2 mg; niacin, 1,400 mg.
[3] Mineral premix provides per kilogram ration: iron, 42 mg; manganese, 19 mg; zinc, 50 mg.
[4] Antibiotic premix provides 55 mg terramycin per kilogram of ration.
[5] Nine parts glucose to one part Ethoxyquin.

EXPERIMENT III

A third experiment was conducted using Rations I and III, to confirm the previous observations. Ten lambs were placed on each treatment at 2 days of age. The ration formulations were the same as those in the previous experiment and contained 24% protein, 20% fat, vitamins, minerals, antibiotic, and antioxidant. A mixture of the dry ration with water (1:5) was fed

TABLE 4.—Experiments II and III. Weight gains of lambs fed either control milk replacer rations or those containing fish solubles and soy flour.

	Experiment II			Experiment III	
	Control	Fish solubles	Fish solubles + soy flour	Control	Fish solubles
Average weight gain, kg					
Initial	5.64	6.59	5.77	4.88	5.20
14 days	1.72	1.00	0.36	3.13	1.04
28 days	4.50	3.59	1.27	5.75	3.01
Average daily weight gain, g					
14 days	120	70	30	220	70
28 days	160	130	40	200	100

throughout the entire experiment which was terminated after 28 days.

Table 4 shows the results of this experiment. The average daily weight gains of lambs fed the control ration and those fed the fish solubles plus milk products ration were 200 g/day and 100 g/day, respectively. The combined results indicate that the ration containing 15% freeze-dried menhaden solubles only produced a 58% growth response as compared to that of the control ration. At the 15% level of incorporation, dried fish solubles will not effectively replace the DSM protein. It should be noted that this level of incorporation corresponds to 30% on an "as is" basis (before freeze drying) which is an extremely high feeding level for fish solubles.

The College Park Laboratory is continuing to study the feasibility of using fish proteins, such as partially hydrolyzed press cake, defatted fish meal, and lower grade forms of FPC as substitutes for milk products in liquid rations for neonatal animals.

CONCLUSIONS

The data indicate that a higher quality protein than that in fish solubles is necessary in order to incorporate significant quantities of fish protein in milk replacer rations.

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COMPARISON OF THE ASSIMILATION OF DIFFERENT DIETS BY *PENAEUS SETIFERUS* AND *P. AZTECUS*

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ABSTRACT

Juvenile penaeid shrimp showed high and comparable assimilation efficiencies (80-85%) on a variety of plant and animal diets. In general assimilation efficiencies for proteins and lipids were consistently high; for carbohydrates, low. Organic assimilation per gram organic weight of white shrimp, *Penaeus setiferus*, proceeded at 3.7 mg hr^{-1} on an axenic diatom and 8.4 mg hr^{-1} on an artificial diet. The assimilation efficiency was lower for shrimp feeding on the algal mat coating *Spartina alterniflora* than on two components of the mat. Feeding mechanisms and probable natural diets are discussed as a basis for further study.

In tidal estuaries where consumers are heavily dependent on an input of autochthonous and allochthonous detritus, the trophic structure is obscured by the seemingly omnivorous habit of many of the residents. Historically, the feeding habits of these omnivores have been investigated by examination of gut contents, correlation of numbers of omnivores with type of benthic community, and comparison of the types of foods available in different areas with the species composition of consumers (Darnell, 1964; Corner and Cowey, 1968; Edmondson and Winberg, 1971). While these investigations have been valuable and are the bases of our present understanding of estuarine communities, it should be noted that a large percentage of the foregut contents of many estuarine species is unidentifiable (Darnell, 1964).

In Louisiana estuaries shrimp is seasonally one of the dominant organisms and commercially the most important one. Although speculation about the diet of juvenile shrimp in inland waters has been widespread, the datum base in the literature for these speculations is not convincing. Studies of shrimp gut contents (Flint, 1956; Darnell, 1964) seem to indicate that the organism ingests the dominant materials in the sediments. In Lake Ponchartrain, for instance, Darnell (1961) found that 58% of the stomach contents of adult white shrimp was unidentifiable detritus. Little is known, however, about the ability of shrimp to digest different food sources. Nose (1964), working with *Penaeus japonicus*, reported a higher assimilation efficiency of animal than of plant proteins. Fujii et al. (1963) and Dall (1965) have studied the activity of digestive enzymes of several species of shrimp.

This study concerns the assimilation by the white shrimp, *Penaeus setiferus*, and the brown shrimp, *P. aztecus*, of the organic components of four different defined diets and a natural substrate. Except for the rates reported, the assimilation parameters were measured by a modification of the ratio method of Conover (1966a). Therefore, quantitative recovery of food or feces was not required.

METHODS AND MATERIALS

CALCULATION OF ASSIMILATION PARAMETERS OF ORGANIC MATERIAL

Direct calculation of net assimilation is difficult in aquatic environments because of the need to measure quantitatively both ingestion

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and egestion of food by the organisms under study. Recently, this problem was circumvented by Conover (1966a). He developed a method for determining the net assimilation efficiency of organic matter (U')[3] without quantitative recovery of either the uneaten food or the feces, based upon the assumption that the assimilation process affects only the organic portion of the food. This is a critical assumption since the ash in the food is treated as an inert label to measure the quantity of food ingested. If this assumption is made, the general definition of assimilation efficiency,

$$U' = \frac{(I - N)}{I} \times 100 \qquad (1)$$

where I is the organic weight ingested, and N is the organic weight egested, reduces to Conover's equation,

$$U' = \frac{(F' - E')}{(1 - E')\ (F')} \times 100. \qquad (2)$$

$F' = I/F$ = ratio of organic weight to dry weight of food ingested, and $E' = N/E$ = ratio of organic weight to dry weight of material egested. Symbols are defined in Table 1. Conover (1966a) and Corner, Cowey, and Marshall (1967) found close agreement between assimilation efficiencies calculated by the ratio method and direct quantitative recovery of food and feces. In both cases the comparison was made with zooplankton feeding on phytoplankton.

Assimilation, however, is a complex function controlled by (1) the net assimilation efficiency (U'), or digestibility; (2) the concentration of ash; and (3) the rate of ingestion. For our work, we found it helpful to modify Equation 2 to consider (a) the combined effect of digestibility and organic concentration upon the amount of food assimilated and (b) the net assimilation rate. A further modification was required to consider the assimilation of specific organic moieties. The reasoning and equations are presented briefly below. A more detailed derivation can be found in Condrey (1971).

[3] Conover uses the term "assimilation efficiency." Strictly this should be "net assimilation efficiency" since it measures the difference between assimilated organics and previously assimilated organics which are lost in the feces (peritrophic membrane, digestive secretions). The two terms are used interchangeably in this paper.

TABLE 1.—List of symbols.

Symbol	Explanation
A	Net organic weight assimilated.
A_X	Net amount of an organic moiety assimilated.[1]
E	Dry weight of feces.
E'	Ratio of organic weight to dry weight of feces. (N/E).
e'_X	Ratio of organic moiety to dry weight of feces.
F	Dry weight of food.
F'	Ratio of organic weight to dry weight of food. (I/F).
f'_X	Ratio of organic moiety to dry weight of food.
I	Organic weight ingested.
I_X	Quantity of an organic moiety ingested.
N	Organic weight egested.
N_X	Quantity of an organic moiety egested.
R	Ratio of organic weight to oxidizable carbon.
r_i	Ratio of an organic moiety to total organic weight of food. (I_X/I).
r_n	Ratio of an organic moiety to total organic weight of feces. (N_X/N).
U'	Percent assimilation efficiency of total organic weight $(A/I)(100)$.
U'_X	Percent net assimilation efficiency of an organic moiety. $(A_X/I_X)(100)$.

[1] When denoting a specific organic moiety the subscript X is replaced by P for protein, L for lipid, CH_2O for carbohydrates, C for oxidizable carbon.

FEEDING EFFICIENCY

A comparison of the amount of organic matter assimilated per unit of diet ingested is:

$$A/F = (F')\ (U'/100). \qquad (3)$$

This is a valuable type of representation for simultaneous comparison of the relative organic weight assimilated on different diets, as is demonstrated in Figure 1. The ratio is termed "feeding efficiency" for lack of a better term. Note that whereas U' is a ratio of organic weight assimilated to organic weight ingested, the feeding efficiency considers the effect of differing organic concentrations in the diet. As will be shown, this may be of considerable importance when comparing net assimilation of diets sim-

ilar in organic content but differing in ash concentration.

NET ASSIMILATION RATE

Where either the ingestion or egestion rate is determined, Equation 2 can be readily adapted to yield the net assimilation rate. For the latter case, the organic weight egested (N) is defined as the product of the ratio of organic matter to dry weight egested (E') and dry weight egested (E). Net assimilation, in terms of egested material, is

$$A = \frac{(E)\,(E')\,(U')}{(100 - U')} \qquad (4)$$

where $(100 - U')$ is the percentage of ingested organic food that is egested. When E is reported in terms of dry weight of feces deposited per unit time, Equation 4 yields the rate at which net assimilation of organic matter proceeds.

ASSIMILATION PARAMETERS FOR SPECIFIC ORGANIC MOIETIES

NET ASSIMILATION AND FEEDING EFFICIENCIES OF AN ORGANIC MOIETY

The determination of the net assimilation efficiency of an organic moiety (U'_x) independent of U' is not possible by direct substitution in Conover's equation (Equation 2). This becomes clear if one considers the equation for net assimilation efficiency of a specific organic moiety.

$$U'_x = \frac{I_x - N_x}{I_x} \times 100 \qquad (5)$$

where I_x is the amount of the moiety ingested and N_x the amount of the moiety egested. Conover was able to derive Equation 2 from Equation 1 by setting I equal to total particulate matter egested minus its ash. Clearly this relationship does not hold for I_x and N_x in Equation 5.

Let r_i and r_n be ratios of the weight of the organic moiety of interest to the total organic weight of the food and feces respectively. Then

$$I_x = r_i I = r_i(FF'), \qquad (6)$$

and

$$N_x = r_n N = r_n(FF')\,(1 - U'/100). \qquad (7)$$

Substituting in Equation 5:

$$U'_x = \frac{r_i - r_n\ (1 - U'/100)}{r_i} \times 100. \qquad (8)$$

From Equations 6 and 7 the feeding efficiency of an organic moiety is:

$$A_x/F = F'\ [r_i - r_n\ (1 - U'/100)]. \qquad (9)$$

NET ASSIMILATION RATE OF AN ORGANIC MOIETY

The amount of a particular organic moiety egested can be defined as

$$N_x = (E)\,(E')\,(r_n). \qquad (10)$$

Similarly,

$$I_x = \frac{(E)\ (E')\ (r_n)}{(1 - U'/100)}\ . \qquad (11)$$

When E is defined as the amount of feces deposited per unit time, Equations 10 and 11 become rate equations for determining the amount of a moiety ingested and egested per unit time. The assimilation rate of the moiety is the difference between the values of I_x and N_x.

EXPERIMENTAL TECHNIQUES

FEEDING

Juvenile shrimp, *Penaeus setiferus* and *P. aztecus*, 24 to 83 mm long, were collected from Barataria Bay, La., and maintained in aerated aquaria containing acid-washed quartz sand, filled with membrane-filtered bay water at 20°-23°C.

Test foods were given to shrimp which had been starved for 12 hr, in groups of 10 to 14, unless otherwise noted. Animals were allowed to feed ad lib. for 12 to 36 hr. Fecal material

was collected soon after voided with a fine-tipped eye dropper. It was placed in a Syracuse dish in saline solution (0.6% $CaCl_2$, 2.5% NaCl) and, under a dissecting microscope, cleaned of all adhering extraneous material such as sand grains. Torn or broken strands were rejected. To remove adherent salts, the fecal material was then washed with 3% ammonium formate on preignited, washed, and tared glass fiber filters and dried at 65°C to constant weight. Reproducibility of blank filters washed with two 1-ml aliquots of 3% ammonium formate varied from 0.01 to —0.05 mg. No correction was made for the sporadic weight loss of the blanks. Dried samples were frozen until analyzed. Sufficient fecal material was obtained for 2-8 replications of each analysis. Analyses of the fecal pellets produced on the detritus diet used 0.2 to 1 mg samples. The high variability of results with these samples was greatly reduced by increasing sample size. Therefore, subsequent analyses of fecal material employed 1 to 10 mg feces per replication. Errors in samples less than 1 mg in weight were presumed to be caused by inhomogeneity of fecal material and magnification of the absolute errors involved in weighing and chemical analyses. Replications for each analysis were chosen from fecal samples collected at different feeding intervals. There was no indication of a change in the assimilation efficiency of a given diet with time.

To avoid undue handling, shrimp were sized and identified to species only after feeding. Therefore, feeding occurred with mixed sizes and species. Three diets—diatom, Chow, and algal mat—were fed to white shrimp only, and two diets—detritus and AF-1—were fed to white and brown shrimp. In tests in which individual shrimp were fed differences were not found in assimilation efficiency due to size (see for instance Table 7) or species. Therefore, the results reported here are assumed to apply equally to both species within the size range used.

FEEDS

The digestibility of four defined diets, two artificial and two natural, was investigated. In addition, in a fifth test, shrimp were allowed to graze on the algal community coating the base of culms of the oyster grass, *Spartina alterniflora*, and the assimilation of this food source was measured.

The four defined diets were: (1) an axenic culture of the periphyton diatom, *Cylindrotheca fusiformes*; (2) a heavily bacterized culture of the same diatom (termed hereafter "detritus"); (3) AF-1,[4] an artificial food consisting of rice bran (52.0%), shrimp meal (30.5%), fish meal (8.0%), fish solubles (2.0%), mineral mix (2.0%), soy protein (3.0%), and Calgon (0.2%); and (4) Trout Chow,[5] consisting primarily of fish meal, fish solubles, soybean meal, ground wheat, and ground yellow corn, with a guaranteed minimum analysis of 40% crude protein, 2.5% crude fat, and 5.5% crude fiber.

The method used rests on the assumption that the food is representative of the ingested material, that is, that selection does not occur. In order to minimize the possibility that the shrimp could select by sorting of particles, and to prevent dispersion and suspension of the defined diets during feeding, all these diets were bound by mixing with a 2% algin solution (Meyers, Butler, and Hastings, 1972). The mixture was extruded through a syringe of 1-mm pore diameter into a 0.6 to 1.2% $CaCl_2$ solution. The calcium ion sequestered the algin, producing either strands or small spheres of bound food which were readily accepted by the shrimp. Details of this method are discussed at length in the aforementioned article.

CHEMICAL ANALYSES

After drying, samples of food and feces were digested along with the glass fiber filters on which they were isolated. Filter blanks carried through the same analytic procedures indicated no detectable contamination from this source.

[4] Prepared by Dr. Samuel P. Meyers and D. Butler, Department of Food Science, Louisiana State University, Baton Rouge, La.

[5] Ralston Purina Company, St. Louis, Mo. Reference to trade names in the publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

Oxidizable carbon analyses were by the wet dichromate procedure of Johnson (1949) as reviewed by Strickland and Parsons (1968). Glucose was used as a standard. The limitations of this method are discussed by Johnson (1949). Total nitrogen was determined by a micro-Kjeldahl technique with ninhydrin color development; lipids in terms of fatty acids by saponification followed by complexing with pinacyanol; and carbohydrates in terms of glucose using the anthrone reaction. Methods are those described by Strickland and Parsons (1968). Protein was estimated by multiplying the nitrogen values by 6.25.

Ash-free dry weights were determined from samples heated to dryness after addition of 1 ml of nitric acid and then ignited at 500°C (2 hr). For the defined diets (i.e., diatom, detritus, AF-1, and Trout Chow), F' values were obtained from samples treated in this manner. Because of small sample size, accurate determinations of ash-free dry weight could not be made for fecal material. Therefore E' was calculated from oxidizable carbon in the feces, assuming that the ratio of total organic weight to oxidizable carbon (R) determined for the food was true also for the feces. Markedly different diets yielded a ratio of oxidizable carbon to organic weight of 1.92 to 2.33 (Table 2). This gives an estimate of the likely error involved in the assumption. Insufficient material was obtained from the algal mat for ash-free dry weight determination of F', and this value was estimated by multiplying the oxidizable carbon concentration by 2.

Analyses of variance were performed on the raw data and are shown as standard errors of the mean in the appropriate tables.

RESULTS

The effect of using 10 to 14 shrimp as a group in each test was to average individual variation. As shown in Table 3 variation in fecal analyses among subsamples within the tests was extremely low, the coefficient of variation usually less than 5%. Individual variability is shown in the results of the feeding study on a natural algal mat (Table 8). In this test, the substrate presented to the shrimp was not homogeneous. The coefficient of variation of U' for individual shrimp fed on diets ranging from 20 to 31% oxidizable carbon was 16%.

Comparison of total organic concentration to the sum of protein, lipids, and carbohydrate re-

TABLE 2.—Chemical analyses of defined diets.

Diet	Total organic wt	Oxidizable carbon	Organic wt	Nitrogen	Nitrogen	Lipids	Lipids	Carbohydrates	Carbohydrates
	Dry wt	Dry wt	Oxidizable carbon	Dry wt	Organic wt	Dry wt	Organic wt	Dry wt	Organic wt
	F'	f'_C	R	f'_N	r_i	f'_L	r_i	f'_{CH_2O}	r_i
	%	%		%	%	%	%	%	%
Diatom	85 ± .01[1]	43 ± 1.2	1.98	7.6 ± .04	8.9	19 ± 1.4	22	5.7 ± 0.4	6.7
Detritus	80 ± .06	42 ± 1.1	1.92	5.1 ± .46	6.4	20 ± 4.8	25	11 ± 0.4	14
AF-1	82 ± .00	35 ± 1.3	2.33	5.4 ± .00	6.6	7.4 ± 1.3	9.1	20 ± 0.3	24
Chow	89 ± .00	46 ± 2.1	1.93	7.2 ± .06	8.1	4.6 ± 0.1	5.1	25 ± 0.0	28

[1] Figures are mean values from 2-8 determinations ± standard error.

TABLE 3.—Chemical analysis of feces produced by shrimp fed on defined diets.

Diet	Oxidizable carbon	Nitrogen	Nitrogen	Lipids	Lipids	Carbohydrates	Carbohydrates
	Dry wt	Dry wt	Organic wt	Dry wt	Organic wt	Dry wt	Organics
	e'_C	e'_N	r_n	e'_L	r_n	e'_{CH_2O}	r_n
	%	%	%	%	%	%	%
Diatom	22 ± 1.1	2.4 ± .00	5.6	0.69 ± 0.1	1.7	9.1 ± 1.3	21
Detritus	20 ± 6.2	4.1 ± .10	10.7	8.1 ± 0.9	23	13 ± 1.5	35
AF-1	29 ± 1.3	3.4 ± .02	5.1	3.3 ± 0.3	5.0	18 ± 2.4	27
Chow	32 ± 0.8	3.4 ± .02	5.5	3.5 ± 0.1	5.7	21 ± 2.2	34

vealed that in the foods 75 to 85% of organic weight was accounted for. These results were consistent, indicating the presence of organic components which are not detected by any of the three methods. Recovery of organic fractions from fecal material was, with the exception of the detritus diet, lower than with foods, ranging from 60 to 74% of organic weight of the feces. The implication is that the unaccounted organic components of the food are also poorly assimilated by shrimp and accumulate in the feces. We have not been able to identify the chemical nature of these components.

DEFINED DIETS

Net Assimilation Efficiency of Total Organic Weight and of Organic Moieties

Tables 2 and 3 show results of chemical analyses of the defined diets and of the feces of shrimp fed on these diets. Data are presented not as amounts, but as percentages for incorporation into the ratio equations.

Assimilation efficiencies calculated from these data (Table 4) revealed that the organic matter of three of the diets was assimilated with a high degree of efficiency. These diets were the diatom, 87%; the detritus, 85%; and the Chow, 80%. The similarity in overall digestibility suggests an adaptive trituration and enzymatic apparatus operating as efficiently against diatom frustules as against bacterial cell walls. The ability to assimilate effectively varied diets of animal, vascular plant, and algal origin denotes the true omnivorous habit of the shrimp.

TABLE 4.—Net assimilation efficiencies of total organic matter, protein, lipids, and carbohydrates for shrimp fed on defined diets.

Diet[1]	Total organic wt U'	Proteins U'_P	Lipids U'_L	Carbohydrates U'_{CH_2O}
	%	%	%	%
Diatom	87	92	99	59
Detritus	85	75	86	63
AF-1	55	65	75	49
Chow	80	86	78	76

[1] Diatom and Chow diets were fed to white shrimp, and detritus and AF-1 diets were fed to white and brown shrimp.

Although the two artificial diets were comparable in chemical analyses, the overall digestibility of AF-1 (55%) was low compared with the Chow. According to Brazka (in Edmondson and Winberg, 1971), this indicates either a "specific barrier" in digestion of the diet or superfluous feeding. Of the components of AF-1, the shrimp meal, because of its high chitin content, may be the cause of the inefficiency of assimilation.

In general, lipids and proteins were digested with a higher efficiency than total organic assimilation while carbohydrate assimilation lagged. The main exception to these generalizations was the detritus protein, which was assimilated with an efficiency of 75% compared to 85% for U'. Bacterial cell walls reportedly account for from 10 to 40% of the dry weight of the cells and are composed of as much as 75% protein (Pelczar and Reid, 1965). The lower digestibility of detritus protein may be due to an enzymatic inability to attack the compacted cell wall protein. However, the results for this diet are not clear since the assimilation efficiencies for the specific organic moieties are all equal to or lower than U'. This implies either that (1) the correction factors and standards employed were not representative of the organic moieties present in the samples or that (2) an unmeasured fraction of the total organic weight was assimilated with a higher efficiency than the total organic matter. These difficulties are inherent in any general analysis of this type and indicate the necessity for care in interpretation of results.

For protein digestibility our results are considerably higher than those of Nose (1964), who used a chromium oxide tracer to study assimilation of protein by *Penaeus japonicus*. On a diatom diet he found a U'_p of 62.5%; on *Ulva*, a green alga, a maximum of 30%. The experiments are difficult to compare with ours because Nose also found a direct proportionality between nitrogen content of the diet and U'_p. Assimilation efficiency of protein increased with diet nitrogen. His diatom and *Ulva* diets were 1.36 and 1.64% nitrogen, respectively, compared to our analyses of 7.6% in *Cylindrotheca fusiformis*. At the diet nitrogen concentration we measured one would expect, using the proportional-

ity Nose demonstrated, a U'_p of about 80% compared to our observed value of 92%. Thus his low values for protein assimilation on plant diets may have been a function of the low nitrogen analysis of the food rather than an inherent inability of shrimp to digest plant proteins efficiently.

Feeding Efficiency

Feeding efficiency (grams assimilated per gram dry weight of particulate material ingested) is presented in Figure 1 and Table 5. As is demonstrated by the figure, the magnitude of the assimilation efficiency of an organic moiety itself may be misleading, as its nutritive value depends not only on digestibility but also on its concentration in the food. For instance, in the diatom diet the lipids were assimilated with an efficiency of 99%, but the feeding efficiency was only 19% (when expressed as milligrams per milligram of food × 100). Furthermore, although in this diet the lipid fraction was the most readily assimilated, twice as much protein as lipid was assimilated per unit dry weight ingested. Also although the digestibility of AF-1 carbohydrates was the lowest of the four diets ($U'_{CH_2O} = 49\%$), feeding efficiency for carbohydrates was higher than from either the detritus or the diatom because of the high carbohydrate concentration in AF-1. For the defined diets feeding efficiency parallels U' because of their high and comparable ash-free dry weights.

TABLE 5.—Feeding efficiency—the assimilation of total organic weight, protein, lipid, and carbohydrate per milligram dry weight of diet ingested.

Diet	Total organic wt A	Proteins A_P	Lipids A_L	Carbohydrates A_{CH_2O}
	μg	μg	μg	μg
Diatom	740	440	190	34
Detritus	680	240	170	70
AF-1	450	210	56	97
Chow	710	390	35	190

Minimum Rates of Net Assimilation

In tests with *C. fusiformis* and Trout Chow diets, fecal pellets were recovered quantitatively over 36- and 12-hr feeding periods, respectively. Because a small but undetermined amount of fecal material was lost, the fecal release rates reported for these diets are minimal. As is shown in Table 6, defecation of shrimp when fed

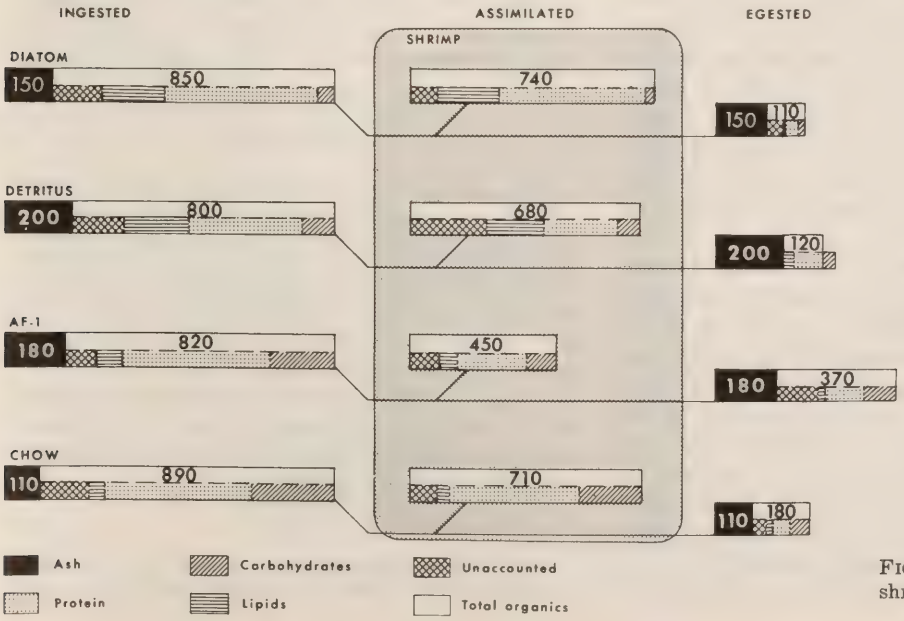

FIGURE 1.—Organic budget of shrimp fed on defined diets.

TABLE 6.—Minimum fecal release rates[1] of *Penaeus setiferus* fed on *Cylindrotheca fusiformis* and Chow.

Diet	Fecal release rate	Dry wt shrimp	Percent organic wt shrimp	Fecal release rate
	mg/hr	*g*	%	*mg/g organic shrimp/hr*
Diatom	5.79	5.09	83	1.3
Chow	9.06	3.15	83	3.4

[1] Calculations give minimum fecal release rates because some small loss of feces may have occurred.

on *C. fusiformis* proceeded at a minimal rate of 1.3 mg dry weight per gram organic weight of *P. setiferus* per hour. With the Chow, the release rate was more rapid, 3.4 mg hr^{-1}.

The minimal fecal release rates were employed to determine the rates at which total organic assimilation and assimilation of organic moieties occurred. These values (Table 7) reflect all three assimilation parameters, that is, digestibility, concentration in the food, and ingestion rate. The similarity in digestibility and total organic and protein composition of the two diets (see Figure 1) was obscured by the higher ingestion rate on the Chow. When viewed in time, net assimilation of organic material proceeded more than twice as fast on the Chow as on the diatom.

The protein assimilation rate followed a pattern similar to the rate of assimilation of total organic material; however, because of the high Chow carbohydrate analysis, sugars were assimilated more than 13 times as fast from the Chow than from the diatom. Conversely, even though ingestion of the diatom diet was relatively slow, its high concentration of easily digested lipids resulted in a faster assimilation of lipids than from the Chow.

We have reported assimilation rates in terms of the organic content of the feeding penaeids so that these rates are indicative of rates of replenishment. Johannes and Satomi (1967) reported the rate of net assimilation of *Nitzschia closterium* by *Palaemonetes pugio*, the grass shrimp, as 1.3 mg organic carbon per gram dry weight *P. pugio* per hour. This is somewhat lower than the rate we measured for *Penaeus setiferus* on *C. fusiformis* (2.1 mg oxidizable carbon per gram dry weight per hour). Johannes and Satomi employed quantitative recovery of food and feces rather than the ratio method.

TABLE 7.—Minimum rates of ingestion, net assimilation, and egestion of total organic weight, protein, lipid, and carbohydrate per gram organic weight *Penaeus setiferus*.

Diet	Organic moiety	Ingested *I*	Assimilated (net) *A*	Egested *N*
		mg hr^{-1}	*mg* hr^{-1}	*mg* hr^{-1}
Diatom	Total organic wt	4.3	3.7	0.6
	Protein	2.4	2.2	0.2
	Lipid	0.92	0.91	0.01
	Carbohydrate	0.29	0.17	0.12
Chow	Total organic wt	10.5	8.4	2.1
	Protein	5.3	4.6	0.7
	Lipid	0.53	0.41	0.12
	Carbohydrate	2.9	2.2	0.7

The rate of organic assimilation is not necessarily proportional to the rate of incorporation into body tissue. However, for an omnivore feeding on a richly diverse flora and fauna, mutual compensation should prevent the nutritional imbalance of any specific food from exerting a profound effect (Provasoli, Shiraishi, and Lance, 1959). The data make clear the distinction between digestibility (U') and assimilation rate. The latter is a function of both U' and ingestion rate. A rapid ingestion rate can compensate for low digestibility. For example, Meyers[6] has preliminary growth experiments which suggest that the growth rate on AF-1 is high although U' on this diet is low (Table 4).

ALGAL MAT

In order to estimate the ability of the shrimp to graze a naturally occurring food material, white shrimp were allowed to feed individually on the algal mat coating *Spartina alterniflora* culms. This mat consisted mostly of diatoms and filamentous green algae growing on and among the red algae *Polysiphonia* and *Bostrichia*. Such communities are found on the bottommost foot of the streamside *Spartina* in many shallow brackish water bays along the southeastern Louisiana coast.

[6] Personal communication, Dr. Samuel P. Meyers, Louisiana State University, Baton Rouge, La.

Penaeids were able to remove sections of the algal mat from the surface of *S. alterniflora* with either the mandibles, or the mandibles and the first and second walking legs. These sections were then rotated in the mandibular area by the maxillipeds. Rejection of uningested particles occurred in the mandibular region. At no time was regurgitation of particles entering the proventriculus observed.

Despite rejection of portions of the mat, the concentration of oxidizable carbon in the algal mat presented to each shrimp was employed as an approximation of oxidizable carbon ingested. Thus, in this test we were unable to account for selection. Table 8 shows the concentration of oxidizable carbon occurring in the mat and feces.

TABLE 8.—Net assimilation efficiencies of individual *Penaeus setiferus* fed on algal mat.

Shrimp length	Algal mat oxidizable carbon	Feces oxidizable carbon	AU'[1]
	Dry wt[2]	Dry wt	
mm	%	%	%
24	24	8.0	80
30	25	9.4	77
32	22	11	64
35	20	11	56
36	22	12	62
37	26	8.6	81
40	22	14	52
42	29	16	66
44	31	13	76
Mean			68
Standard deviation	3.6	2.6	10.7

[1] A ratio of organic weight to oxidizable carbon of 2 was chosen to convert oxidizable carbon to total organic weight.
[2] Individual values recorded have a coefficient of variation of 10%.

Assimilation efficiency ranged from 52 to 81%, with a mean of 68%. The feeding efficiency (Figure 2) was 33%. Thus, digestibility of the algal mat appears to be lower than that of two of its constituents, i.e., *C. fusiformis* and detritus. The lower (68%) U' for the algal mat compared to the defined diets may be explained by the following considerations. First, the green and red algae present in the mat have cellulose cell walls which are probably not digestible, or may be more resilient to trituration, by the shrimp. Second, the ash content of the mat was about 50%, and Conover (1966b) has reported an inverse relationship between ash content and digestibility of various algal diets ingested by *Calanus hyperboreus*. A third possibility concerns the rejection of portions of the mat as a means of selection. The occurrence in the rejected material and in the feces of the same algal species indicated that rejection was not a method of selection for specific organisms. However, the rotation of the detached mat in the mandibular area close to the excurrent respiratory stream appeared to result in removal of adherent silt. If this observation is valid, the organic fraction in the algal mat as it occurs on *Spartina* would be lower than that of the ingested material, and efficiencies of net assimilation and feeding would have been underestimated in this study.

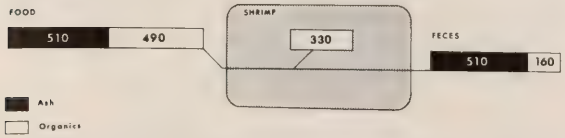

FIGURE 2.—Organic budget of shrimp fed on algal mat.

CONCLUSIONS

The results of this study and others begin to form a picture of the feeding process in shrimp, which is still far from complete, but does explain some of the observed phenomena. We describe this process for a shrimp feeding on an algal-microbial community such as that described above, not as a definitive statement but as a hypothesis for further testing.

A portion of the mat is torn off by the first and second walking legs and passed to the maxillipeds. Rotation of the mat in the proximity of the excurrent respiratory stream results in washing most of the silt away from the periphery of the mat. Once cleaned, the peripheral area is torn off by the mandibles and ingested. Thus selection for organic material occurs. Continued rotation of the mat entangles the inner algal filaments and silt into a ball. This knotting of the filaments impedes further silt removal. At this point, the uningested portion is rejected.

Ingested material enters the proventriculus where it is ground between the teeth of the gastric mill and forced through the filter press into the digestive gland (Dall, 1967). Passage of the ingested material through the proventriculus is governed in part by the time required for this trituration. As the digestive gland fills, ingestion slows. Thus the ingestion rate is governed by the filling of the digestive gland which is in turn regulated by the time required to render the food small enough to enter this organ. In this respect the shrimp is viewed as a conservative grazer, ingesting no more than it can effectively assimilate at one time (see Corner and Cowey, 1968, on the question of superfluous feeding.)

The assimilation of an organic moiety is a function of (1) the activity and concentration of the digestive enzymes of the shrimp and (2) the form of the moiety in a specific diet. Differences in rates of assimilation of different organic moieties indicate that lipases and proteinases are more active in the shrimp's digestive processes than are carbohydrases. The form of the moiety determines its susceptibility to catalytic attack. For instance, the diatom lipids were assimilated almost entirely (99%); whereas assimilation efficiency of the detritus lipids, which occurred at about the same concentration in the diet, was 86%. We suggest that lipids in the diatom occur primarily as oil droplets in the cell and are easily leached and attacked by lipolytic enzymes. Incorporation of the lipids into structural materials such as cell membranes in bacteria could make them less accessible by enzymes and reduce assimilation efficiency. For structural components of a diet, then, assimilation efficiency would be related to the degree of maceration or trituration of the food.

Material not entering the digestive gland passes from the proventriculus to the intestine to be voided at the anus. The physical requirement in the shrimp for material to occupy the space in the proventriculus above the filter press probably places a mechanical limit upon its assimilation efficiency.

The results suggest three generalizations concerning the type of diet shrimp may be expected to feed on in the natural environment. (1) Juvenile shrimp exhibit a high and comparable assimilation efficiency on a variety of plant and animal materials. (2) Proteins and lipids are, in general, assimilated more efficiently than carbohydrates. (3) Rates of assimilation on different material vary, and this variability is considered to be related to how rapidly the diet can be ground and filtered for assimilation. These generalizations show the shrimp to be a true omnivore in the sense that it is able to assimilate a wide variety of foods. The most digestible food is high in protein and lipids, low in carbohydrates.

Since the animal occurs seasonally in high concentrations in the marsh, its natural diet must be present in large volumes and must be rapidly replenished. Data from our laboratory[7] indicate that the benthic meiofaunal biomass in the Louisiana saline bays is insufficient to comprise a major volume of the shrimp's diet. On the other hand, the rates of production of detritus from the marsh grass *Spartina*, and of the periphyton and benthic communities, have been found to be high (Kirby, 1971; Stowe et al., 1971; Pomeroy, 1959). Thus, of the naturally occurring foods, the benthic algal communities and the detrital microbial communities on dead *Spartina*, because of their rapid turnover rates, appear to be the most likely sources.

ADDENDUM

An excellent article by Forster and Gabbott (1971) was published during final revision of this publication. They investigated the nitrogen and carbohydrate assimilation of certain commercial foodstuffs by *Palaemon serratus* and *Pandalus platyceros*. Nitrogen assimilation of the different diets varied from 80 to 95% whereas the assimilation of simple carbohydrates varied from 66 to 102%. Thus the nitrogen assimilation efficiencies reported in our paper agree with their findings while our carbohydrate assimilation efficiencies are lower.

[7] H. J. Bennett, Louisiana State University, Baton Rouge, La. (Unpublished.)

The primary question raised by Forster and Gabbott for our results is the reliability of Conover's ratio method. They were unable to account for 29 to 40% of the ash, and were not certain whether this was assimilated or lost to solution. With the ratio method assimilation of ash leads to underestimation of assimilation efficiency. For such a case the corrected assimilation efficiency (U'_{correct}) is given by the equation:

$$U'_{\text{correct}} = U'/100 + (A_u/A_f)\,[E'(1-F')/F'(1-E')] \times 100$$

where A_u/A_f is the fraction of ash assimilated. Similarly for U'_X the corrected value is found by the same equation except that the second term is also multiplied by r_n/r_i. From these equations it can be seen that the error incurred by failure to correct for assimilation of ash varies inversely with the ash content of the food and directly with the organic content of the feces. Thus errors are magnified when U' is low. If we assume that the upper limit of ash assimilation reported by Forster and Gabbott applied to our studies, the error in our U' values would be less than 10% for all diets except AF-1, which would have been in error by 35%. Similarly, high U'_X values would have small errors, low values relatively large errors.

We consider it likely that the high apparent ash assimilation of Forster and Gabbott are related to the organism used and the experimental conditions. They point out that loss of ash may have occurred through regurgitation and excretion. These parameters would be important when shrimp are fed for a short period (15 min) and feces collected subsequently over a long period (20 hr). On the other hand in our tests we observed no regurgitation, the shrimp fed continuously, and feces were collected about every 2 hr. These conditions should minimize ash loss.

ACKNOWLEDGMENTS

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NOTES

GROWTH AND FOOD CONVERSION OF RAINBOW TROUT REARED IN BRACKISH AND FRESH WATER

Although brackish water culture of rainbow trout (*Salmo gairdneri* Richardson) has been practiced in other countries for years (Awakura, 1962; Awakura, Shibata, and Honma, 1962; Sato, 1965; Jensen, 1967), few attempts have been made to culture this euryhaline species in brackish water in the United States (Leon, 1970). The following study was designed to study the growth, food conversion, and survival rates of rainbow trout reared from fingerling to market size in brackish and fresh water.

Materials and Methods

Six 1.8-m diameter round fiber glass tanks with a water depth of 0.6 m were used as experimental culture tanks (Andrews et al., 1971). Fresh water from a deep well (22°C) or brackish water (25-30‰) from the Skidaway River, Savannah, Ga., was pumped into each tank through flow control nozzles at a rate of 19 liters/min (1.3 hr/exchange). Since the temperature of the brackish water varied and the experimental tanks were located out-of-doors, water temperatures were not controlled.

Four experimental tanks were stocked with rainbow trout averaging 60 g each at an initial density of 7.2 kg fish/m^3, and two were stocked at a density of 14.4 kg fish/m^3. Fish in two of the tanks containing 7.2 kg/m^3 and the tanks containing 14.4 kg/m^3 were acclimated to brackish water by gradually changing the fresh to brackish water ratio of incoming water. Figure 1 shows the changes in salinity during the 9-day acclimation period.

Each group was fed a commercial pelleted trout feed[1] twice daily according to Leitriz's feeding table (Oshima, 1968). The entire population of each tank was weighed and counted monthly. Temperatures, ammonia, salinity, and dissolved oxygen levels were determined biweekly. Ammonia levels were below 0.3 ppm and oxygen concentrations were above 7.0 ppm throughout the experimental period. After 16 weeks (December 4, 1970-March 26, 1971) the experiment was terminated. Growth data was tested for statistical significance by the method of Duncan (1955).

Results and Discussion

Acclimation to brackish water

A survival rate of 99.5% was obtained in the two groups acclimated to brackish water during the 9-day period and the following 10 days in which salinity was 30‰. These results are in contrast to a previous report that over 40% mortality was obtained when rainbow trout weighing approximately 60 g each were adapted to 30‰ salinity (Oshima, 1968).

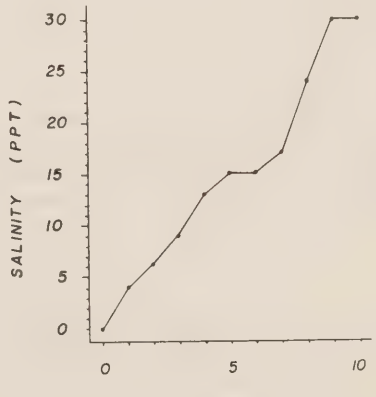

FIGURE 1.—Changes in salinity during the 10-day period in which the rainbow trout fingerlings were acclimated to brackish water.

[1] Donated by Agway, Inc., Syracuse, N.Y.

In a pre-experiment test, 60-g trout were gradually adapted from fresh water to 30‰ salinity within a 1-day period with a mortality of 5%.

These results indicate that a gradual change from 0 to 30‰ salinity over a 10-day period can be accomplished with low mortality. Since other studies have indicated that larger fish are more easily adapted to higher salinities than smaller fish (Awakura, 1962; Sato, 1965), this conclusion only holds for the 60-g fish.

Growth, survival, and food conversion data

Growth curves for the three experimental groups are shown in Figure 2 along with the average water temperatures for the corresponding period. During the first 5 weeks of this experiment when the growth rates of all groups were similar, temperature differences were not as large. Once temperature differences occurred, growth rates were affected. The final average individual weights (256 g) were significantly higher ($P < 0.05$) in the freshwater groups which were maintained at near constant temperature (averaging 21.3°C) than in the colder saltwater (13.5°C) groups (217 g in the low density group and 176 g in the high density group). The average final density (Table 1) was significantly greater ($P < 0.05$) from the highest stocking density tanks in brackish water (Group 2) than from the lower density brackish water (Group 1) and freshwater (Group 3) tanks.

Food effiiciency and survival were best in the lower stocking density brackish water tanks (Group 1) and poorest in the freshwater tanks (Group 3). A gradual mortality of one or two fish daily was observed in the freshwater group which was maintained at temperatures in excess of the optimum temperature for rainbow trout.

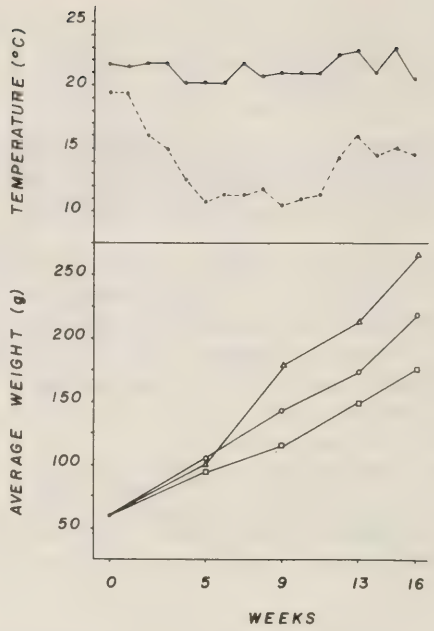

FIGURE 2.—Water temperatures and growth curves from an experiment in which rainbow trout were reared in fresh and brackish waters. The solid and broken lines represent temperatures for the freshwater and brackish water groups, respectively. The triangles represent average weights of the fish in the freshwater group, and the circles and squares represent average weights for the low and high density brackish water groups, respectively.

Temperature had a greater effect on growth, food conversion, and survival than did salinity. The freshwater group maintained at approximately 21°C grew faster than the brackish water group on the individual weight basis, but had

TABLE 1.—Experimental data from the entire 16-week growing period (December 4, 1970-March 26, 1971).

Group	Initial density	Average salinity	Average temperature[1]	Final density[2]	F.C.R.[3]	Percent survival
	kg/m³	‰	°C	kg/m³		
1	7.2	28 ± 0.6	13.5 ± 3.2	24.0 a	1.8	98
2	14.4	28 ± 0.6	13.5 ± 3.2	42.6 b	2.1	93
3	7.2	0	21.3 ± 1.3	27.2 a	2.3	87

[1] Brackish water (incoming) was pumped from Skidaway River which varied in temperature while fresh water was direct from a well and at a constant temperature (22°C).
[2] Values follow by the same letter are not statistically different ($P > 0.05$).
[3] Food conversion ratio (grams feed/gram gain).

a poorer food conversion efficiency and survival rate. The lower survival rate (87%) of this group resulted in a total production (final density) only slightly greater than the saltwater group stocked at the same density.

A faster growth rate, better survival, and better food conversion were obtained at the lower stocking density brackish group thus demonstrating the effects stocking density has on these variables. The fact that oxygen was over 7 ppm in all groups throughout this experiment indicates that stocking density and not oxygen stress accounted for this reduction in performance.

Conclusions

The fact that temperature was not constant in all groups precluded a conclusive comparison of the performance of rainbow trout in brackish and fresh water. Nevertheless, the following conclusions can be made from these experimental data:

1. Rainbow trout were converted from fresh to 30‰ salinity in a period of 9 days and were reared to market size at this salinity.
2. Trout fingerlings averaging 60 g each were reared to 266 g in 21°C fresh water with a rapid individual growth rate and an acceptable survival and food conversion rate.
3. Survival and growth rates and food efficiencies were excellent for trout reared in brackish water at an average temperature of 13.5°C.

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THE AMOUNT OF SPACE AVAILABLE FOR MARINE AND FRESHWATER FISHES

Cohen (1970) has presented rather careful estimates of the total number of fish species in the world and in each of eight ecological groupings. He found that an "astonishingly high percentage" of bony fishes live in freshwater habitats. According to Cohen's analysis, 41.2% (8,275 species) of all fish species live in fresh water (includes both primary and secondary freshwater fishes). He indicates that this high percentage must reflect the degree of isolation possible in freshwater environments and refers to the great variety of habitats and ecological niches in fresh water and also along tropical shores.

The great number of freshwater fish species becomes even more striking if the volume of fresh water in the world is compared to the volume of the oceans. Indeed, the mode of speciation and the structure of the niche appear highly divergent between the two environments. The oceans account for 97% of all the water in the

world whereas the amount of fresh water in lakes and rivers (that which would be available as fish habitat) approaches an almost negligible percentage—only 0.0093% of the world's water (van Hylckama, 1971) (Table 1). In this sense then, 41.2% of all fish species live in less than one one-hundredth of one percent of the available water. Table 2, which is based on Cohen's (1970) data and on the data presented in Table 1, shows the great disparity between freshwater and marine environments in terms of the number of species per unit volume of water. The calculations show that there are about 113,000 km^3 of water per marine species but only about 15 km^3 for each freshwater species, or approximately a 7,500-fold difference. It is, of course, true that a species does not occupy a particular parcel of water to the exclusion of other organisms; nevertheless, it seems conceptually possible and without undue loss of reality to consider that each species has available a certain volume of water which it can occupy. It is known, too, that marine habitats vary greatly from high diversity in tropical shore and coral reef regions to low diversity in open ocean areas (including the deep ocean which constitutes most of the volume of the oceans and in which numbers and biomass greatly decrease with depth). Shore and shelf fishes have about 290 km^3 of water per species compared with about 1,000,000 km^3 for pelagic species (Table 2), or approximately a 3,400-fold difference. If the slope and deep-sea benthic species are added to the pelagic figure, the unit volume of water per species beyond the continental slope is reduced to about 500,000 km^3, which is still a relatively very high figure. The volume of water per species of marine shore and shelf fishes is higher than the freshwater figure by about 20× (290 km^3 vs. 15 km^3). This reflects the similarity in the degree of partitioning in these two regions. Perhaps the number of species per unit volume in the richer tropical reefs exceeds that in a large percentage of freshwater habitats. Also, some marine habitats which are superficially similar to certain freshwater habitats may be expected to have species densities comparable to their freshwater counterparts. Examples might be 1) the deep parts of oceans and lakes (low species density), 2) kelp beds in coastal waters and the vegetated zones of lakes (high species density). It is the open ocean with its broad expanse and great depth that contributes most to the overall very low concentration of species and numbers (discussed below) of marine fishes.

TABLE 1.—Supply (km^3) of water in the world available as fish habitat (from data by van Hylckama (1971)).

Item	Volume	Percent of total
Total water in the world	1,360,000,000	100.0
World oceans	1,320,000,000	97.0
Freshwater lakes	125,000	0.0092
Rivers (at any one time)	1,300	0.0001
(remainder of total is ice, groundwater, atmospheric water, etc.)		

TABLE 2.—Volume (km^3) of water available per species in various habitats.

Type of species	Volume/species
Total marine	113,000
Marine shore and continental shelf to 200 m	290*
Marine pelagic beyond continental shelf	1,000,000
Marine pelagic + continental slope and deep sea benthic	500,000
Total fresh water	15

* The volume of water over the continental shelf was calculated by considering that the shelf underlies 7.5% of the ocean surface (Emery, 1969) and that the average depth over the shelf is about 100 m or 2.5% of the ocean's average depth of 4,000 m.

While it is difficult to estimate the number of fish species in an environment, it is much more difficult to even speculate on the number of individuals per species in either marine or freshwater regions. Gadgil[1] arrived at a figure of 4×10^9 as the average number of individuals per fish species based largely on marine data. Certainly, different marine habitats support widely differing numbers of fishes. Pelagic species such as certain anchovies may attain population levels of 10^{12} whereas some rocky shore species may be several orders of magnitude lower in total numbers, perhaps near 10^6 individuals per species. A figure in the middle of the above two estimates would be 10^9, and in this discussion I have considered 10×10^9 to be the average number of individuals per species in the sea. It

[1] Gadgil, M. On numbers of fish. (Unpublished manuscript) Biology Department, Harvard University, Cambridge, Mass. Present address: Maharashtra Association for the Cultivation of Science, Agarkar Road, Poona 4, India.

is fairly certain, I think, that there are fewer individuals per species among freshwater fishes than among marine fishes. The degree of difference in abundance is, however, difficult to estimate or even imagine. There are some very abundant freshwater species such as certain clupeids and cyprinids, but some are quite rare, most notably the desert cyprinodontids of the southwestern United States which may exist only in the thousands or even hundreds per species.

Two values were used for the average number of individuals per freshwater species—a high value (10×10^9), the same as the figure for marine species, and a low value (10×10^6) which I think is a conservative minimum. A range of values conveys more information in comparing the marine and freshwater situations. The calculations in Table 3 show that marine fishes have $10\times$ to $10{,}000\times$ more space available per individual than freshwater forms, depending upon which freshwater value is chosen. If the lower freshwater figure (10×10^6) is more nearly correct, then the degree of isolation and habitat partitioning in fresh waters becomes even more strikingly apparent. On the basis of total numbers per species, the difference per unit volume between the oceans and fresh water is only 10-fold whereas on the basis of species per unit volume, the difference is approximately 7,500-fold.

TABLE 3.—Volume (km^3) of water available per individual fish in the sea and in fresh water.

Type of species	Number of species	Individuals/ species	Volume/ individual
Marine	11,675	10×10^9	1.1×10^{-5}
Fresh water (1)	8,275	10×10^9	1.5×10^{-9}
Fresh water (2)	8,275	10×10^6	1.5×10^{-6}

The above disparity would seem to be related not only to the degree of isolation but to the relative levels of productivity and biomass in the two environments. Table 4 shows net primary productivity and plant biomass estimates for three major ecosystems: 1) lake and stream, 2) continental shelf, and 3) open ocean. Net primary productivity per unit area in fresh water is about $1.5\times$ to $4\times$ as high as in the sea, and plant biomass per unit area in fresh water is about $2\times$ to $7\times$ as high as in the sea. These figures are perhaps not in great discord with the estimate above that $10\times$ as many fishes occur per unit volume in fresh water as in the sea.

TABLE 4.—Net primary productivity and plant biomass per unit area in three major ecosystems (from data compiled by Whittaker (1970)).

Major ecosystem	Net primary productivity	Biomass
	dry g/m²/year (mean value)	*dry kg/m² (mean value)*
Lake and stream	500	0.02
Continental shelf	350	0.01
Open ocean	125	0.003

These data serve, I believe, to illustrate the quite astounding difference between the amount of space available for freshwater and marine fishes. As Cohen (1970) has emphasized, the calculations also make apparent the need for increased research on freshwater fishes since their habitats are being rapidly modified. In terms of conservation and economic policies, important studies should include those that compare numbers of species and individuals in different local and regional environments in relation to levels of productivity and other factors.

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A SYSTEM FOR COLLECTING LARGE NUMBERS OF LIVE POSTLARVAL PENAEID SHRIMP[1]

Acquiring large numbers of small marine organisms for experimental or commercial purposes is often hampered by inefficient methods. Means for concentrating organisms and separating desired species from the rest of the catch can be particularly troublesome problems.

For commercial shrimp culture and related research, a system is needed whereby large numbers of postlarval shrimp can be efficiently caught, separated, and held alive in a healthy condition. The shrimp of greatest interest for pond culture include the tropical and subtropical species whose habit of entering estuaries during larval stages and remaining there for several weeks makes them accessible in large numbers to various collecting methods. Two general methods are presently employed to collect shrimp for culture. Postlarvae are impounded in the Orient by manipulating tidal flow with sluice gates built into the dikes of ponds (Walford, 1958). This method, however, also impounds undesirable species that enter with the small shrimp. Fishermen of the Philippine Islands catch shrimp larvae by immersing bundles of grass at the edges of mangrove thickets and periodically removing the attached postlarvae with a dip net, or by dipping a triangular net into the water (Caces-Borja and Rasalan, 1968). These methods are time-consuming, and the number of postlarvae caught varies greatly among localities; often catches are too small to provide stock for a successful crop.

The objective of this study was to develop more efficient methods for collecting and separating large numbers of postlarval brown shrimp, *Penaeus aztecus*. Postlarvae of this species immigrate through tidal passes on flood tides from February through September along the Texas coast with peak abundance occurring during late winter and early spring (Baxter and Renfro, 1966). The postlarvae occur in great numbers near the surface, especially in the more shallow areas (Duronslet, Lyon, and Marullo, in press) and are about 11 mm in total length and 1 mm in diameter at immigration.

Description of Equipment

The collecting system, designed for use on a 13-m vessel, is shown in Figures 1 and 2. The telescoping outriggers consist of a pipe frame attached to the vessel and pipe extensions which slide inside the frame. The frame itself was constructed from two pieces of 76-mm (outside diameter) galvanized pipe bolted side-by-side to the top of the cabin. The extensions were 51-mm (outside diameter) galvanized pipe. Holes were drilled in the pipes so that each could be extended 2.4 m and secured with a steel pin.

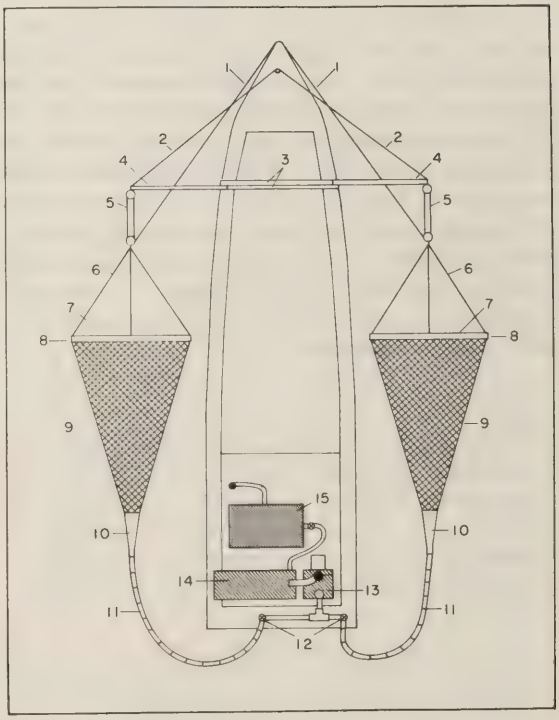

FIGURE 1.—Schematic drawing of collecting system: 1 - bow bridles; 2 - staywires; 3 - outrigger frame; 4 - outrigger; 5 - double block; 6 - net bridle; 7 - trash screen; 8 - net frame; 9 - net; 10 - funnel; 11 - suction hose; 12 - screw valve; 13 - pump; 14 - sorting box; 15 - holding tank.

[1] Contribution No. 336, National Marine Fisheries Service, Gulf Coastal Fisheries Center, Galveston Laboratory, Galveston, TX 77550.

FIGURE 2.—Collecting system in operation on flood tide.

Net frames, 1.2 by 2.4 m, were constructed of 3-mm flat steel reinforced with 6-mm iron rods. Six U-bolts were welded to the frame for the attachment of stainless steel cables which bridled each frame to a double block bolted to the end of each outrigger. The trash screens were made of 6.4-cm square mesh galvanized hardware cloth soldered onto galvanized metal frames which were bolted to the net frame. The nets were fabricated from nylon netting (169 meshes per square inch) measuring 3.7 m in length and patterned so that the seams ran from the corners of the metal frame to the aluminum rings. The rings were attached with bayonet fittings to the collecting funnels. Both the mouth and tail of the nets were reinforced with cotton duck and fitted with brass grommets so that the nets could be laced on the frames and rings.

The collecting funnels were made with 3-mm flat stock aluminum and were 90 cm long (30 cm outside diameter at the mouth and 7.5 cm inside diameter at the tail). A 15-cm nipple was welded to the posterior end where the suction hose from the pump was attached, and a 10-cm flat band was welded to the mouth of the funnel. L-shaped slots were cut in the leading edge of the band. These slots were spaced so that countersunk bolts in the aluminum ring of the net could be inserted and rotated for quick attachment of the net to the funnel.

The self-priming, centrifugal, solids handling pump ("Crown" model PO3LB, Construction Machinery Company, Waterloo, Iowa[2]) was powered by the winch power shaft (Figure 3). In turn, the power shaft was controlled by a small hydraulic motor which allowed regulation of pumping speed. Water volume output could be controlled from 0 to 180 gal/min.

The pump intake pipe was attached to a 7.6-cm (outside diameter) PVC (polyvinyl chloride) tee. A reinforced rubber hose led from each side of the tee to the respective funnel, and a brass screw valve was incorporated in each hose so that we could pump from either or both nets.

The sorting box (Figures 3 and 4) was designed so that the smallest animals caught would be retained and the larger ones discarded. This was accomplished by pumping the catch from the nets onto three sets of sloping screens. A water-jet system was used to keep the animals

[2] Use of trade names in this publication does not imply endorsement of commercial products by the National Marine Fisheries Service.

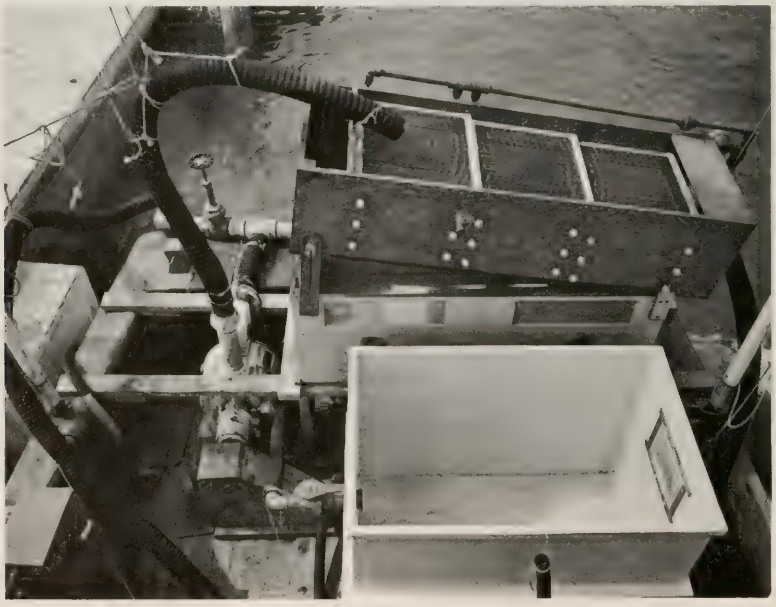

FIGURE 3.—Pump, sorting box, and holding tank.

separated and moving down the screens. The screen frame and the catch box located beneath the screens were made with 19-mm marine plywood. One end of the screen frame was hinged and could be set at the slope providing maximum sorting efficiency. To accommodate excess water, six overflow windows around the top edge of the catch box were screened with fine-mesh netting. The catch box drain emptied into a 145-gal fiber glass holding tank having screened overflow windows (Figure 3).

The 54- by 51-cm screens were constructed of brass welding rods and flat stock aluminum. The rods were cemented in place at both ends along the aluminum strips with liquid solder cement. Excess cement was ground off, and another aluminum strip was bolted to each end, thus sandwiching the brass rods between aluminum strips. Three layers of screens were installed in the frame with each layer having three screens fitted end-to-end so that the rods ran parallel with the long axis of the frame. The average openings between rods for the screen layers were 3, 2, and 1½ mm.

FIGURE 4.—End view of sorting box.

Water-jet pipes were inserted through the walls of the screen frame 5 cm below each screen with two pipes per screen (Figure 3). The pipes were perforated with 2-mm holes spaced 25 mm apart to form the water jets. The force of the jets, which was supplied with water by a 25-mm gasoline-driven centrifugal pump, was controlled by a PVC ball valve on the discharge line of the pump.

Operation of System

After anchoring the vessel, the outriggers were extended, the suction hoses and cones put overboard, and the nets and frames were lowered into the water. A rope was then passed around the bow, and the ends were attached to the bridle of each net. When the nets were subsequently slacked back, the rope bridles became taut, and tidal flow forced the frames into the water (Figure 2). The solids-handling pump and the water-jet pump were then engaged and the jet heights adjusted. When the sorting box was full of water, the valve on the bottom was opened allowing the catch to flow into the holding tank.

Evaluation of System

The number of brown shrimp postlarvae caught per cruise was estimated by periodically taking 5-sec samples from the pump discharge. Twenty collection cruises were made on flood tides between March 17 and June 2, 1971 (Table 1). Numbers of postlarvae caught during individual cruises ranged from 0 to about 106,000, and the total estimated catch for all cruises was about 411,600. Mortalities associated with catching, pumping, and sorting brown shrimp postlarvae were less than 3%.

During evaluation of the system, large numbers of larval fishes and crustaceans other than postlarval brown shrimp were collected. The

more common and readily recognizable forms are listed in Table 2. Mortalities related to capture of these larvae were estimated to be less than 10%, while mortalities for subadults and adults were less than 20%. Large specimens of Atlantic cutlassfish, sea catfish, Atlantic croaker, Gulf menhaden, and the blue crab were passed through the pump with little damage. The sorting box was effective in removing all animals and trash larger than 1.5 mm in diameter, or about 95% of the larval fishes caught. Postlarvae retained in the trash were less than 10% of the total number of postlarvae caught. Larval stages of the blue crab were not effectively separated, however, and were voracious feeders on postlarvae.

This system was efficient in capturing and sorting large numbers of postlarval shrimp and, by adjusting the widths of the sorting screens, can be used to catch and sort most small animals as they migrate through tidal passes. The pump and suction cone attachment on the tail of the nets provided a constant free flow of water which eliminated the problem of clogging or fouling as encountered with standard plankton nets. The system is not restricted to use on a boat and could be easily adapted for land-based operations from piers and platforms.

TABLE 1.—Estimated number of postlarval brown shrimp caught by date in the Bolivar Roads Tidal Pass, Galveston Bay, Tex., 1971.

Date		Fishing time (min)	Number of samples	Estimated total catch
March	17	167	8	14,400
	20	240	9	3,800
	21	50	5	3,000
	22	108	9	5,200
	23	80	6	800
	26	173	16	45,200
	27	345	16	46,200
	28	335	32	52,600
	30	465	49	65,100
	31	180	15	4,500
April	2	173	8	500
	3	150	15	5,100
	7	120	12	200
	13	155	17	9,100
	20	60	6	1,400
	21	135	13	0
	30	100	10	23,200
May	19	160	16	800
	20	220	21	106,000
June	2	90	9	24,500
Total		3,506	292	411,600

TABLE 2.—Fishes and crustaceans collected during evaluation of the system; A = abundant; O = occasional.

Scientific name	Common name	Juvenile	Adult
Anchoa mitchilli	Bay anchovy	A	O
Brevoortia patronus	Gulf menhaden	A	O
Callinectes danae	Gulf crab	O	O
Callinectes sapidus	Blue crab	A	O
Cynoscion arenarius	Sand seatrout	O	
Dysommia sp.	Eel	A	
Elops saurus	Ladyfish		A
Arius felis	Sea catfish	A	O
Gobiesox strumosus	Skilletfish		O
Hippocampus zosterae	Dwarf seahorse		O
Histrio histrio	Sargassumfish		O
Libinia emarginata	Spider crab	O	
Menticirrhus americanus	Southern kingfish	O	
Micropogon undulatus	Atlantic croaker	A	O
Monacanthus hispidus	Common filefish		A
Mugil cephalus	Striped mullet	A	
Ophidion welshi	Crested cusk-eel		O
Palemonetes sp.	Grass shrimp		A
Penaeus setiferus	White shrimp	A	A
Polydactylus octonemus	Atlantic threadfin		A
Porichthys porosissimus	Atlantic midshipman		O
Prionotus tribulus	Bighead searobin		O
Sergistid sp.		A	A
Sphoeroides nephelus	Southern puffer	O	O
Squilla sp.	Mantis shrimp	A	A
Syngnathus scovelli	Gulf pipefish	A	A
Synodus foetens	Inshore lizardfish	A	O
Trachypenaeus sp.	Brokenback shrimp	O	A
Trichiurus lepturus	Atlantic cutlassfish		A

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